An Assessment of the Effects of Streambank Clear-cutting on Macroinvertebrate Communities in a Managed Watershed

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AN ASSESSMENT OF THE EFFECTS OF STREAMBANK CLEAR-CUTTING ON MACROINVERTEBRATE COMMUNITIES IN A MANAGED WATERSHED

by

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ABSTRACT

Culp, J. M. and R. W. Davies. 1983. An assessment of the effects of streambank clear-cutting on macroinvertebrate communities in a managed watershed. Can. Tech. Rep. Fish. Aquat. Sci. 1208: xv + 115 p.

Three macroinvertebrate sampling sites were established on Carnation Creek, Vancouver Island, British Columbia, and sampled from 1974-1980 to determine the effects of logging, with or without buffer zones, on macroinvertebrate communities. Logging without a buffer zone increased streambank erosion and the resulting sedimentation of streambank material caused a significant increase in the proportion of < 9 mm sediment particles in the substrate. Although logging opened the forest canopy and increased the light available for primary production, algal biomass did not increase after logging because phosphorus remained the limiting factor. Allochthonous litter input to the stream was significantly reduced at both logged sites, but the site with a buffer zone provided greater amounts of leaf litter to the stream, and had a higher post-logging benthic standing crop than the site without a buffer zone.

Throughout the pre- and post-logging periods, seasonal changes in macroinvertebrate community composition were strongly affected by the seasonality of discharge: high (winter), low (summer), and transitional (spring and fall). Trophic composition of the macroinvertebrate communities was not affected by logging, with collectors, collector-scrapers and collector-predators numerically dominant during all seasons and years. Logging of the streambank significantly decreased macroinvertebrate densities in the winters, primarily because post-logging sedimentation increased winter scouring. Macroinvertebrate densities at the site without a buffer zone were also reduced in the summer and transitional periods because of sediment intrusion into the substrate and the reduced standing crop of detritus. Macroinvertebrate communities were less detrimentally affected by logging when a < 10 m wide riparian buffer zone and natural debris dams were left along the stream. The buffer zone reduced logging-related scouring in the winter, and leaf litter input in the summer and transitional period was more similar to pre-logging conditions.

Experimental manipulations of substrate particle size, and detritus quality and quantity were conducted in the field, and established that detritus quality and quantity is more important in determining macroinvertebrate distribution and abundance than substrate particle size. The responses to detritus varied between macroinvertebrate taxa, and even among members of the same trophic guild.

Sediment addition experiments were conducted to determine the effect of downstream movement of fine sediments by saltation on macroinvertebrate drift and benthic density. Saltation of sediments increased drift rates and decreased benthic densities, with the timing and pattern of the drift

increases being related to the vertical distribution of macroinvertebrates in the substrate.

Since the streambank of coastal streams provides important energy subsidies to macroinvertebrate communities, and it mediates sediment input to the stream, logging of the streambank is detrimental to macroinvertebrates. Management guidelines must protect the streambank interface with the forest if coastal streams are to be maintained as productive salmon fry rearing habitat.

RÉSUMÉ

Culp, J. M. and R. W. Davies. 1983. An assessment of the effects of streambank clear-cutting on macroinvertebrate communities in a managed watershed. Can. Tech. Rep. Fish. Aquat. Sci. Can. Tech. Rep. Fish. Aquat. Sci. 1208: xv + 115 p.

Trois sites d'échantillonnage de macroinvertébrés ont été choisis le long du ruisseau Carnation, sur l'île Vancouver (Colombie-Britannique) et échantillonnés de 1974 à 1980 pour déterminer les effets de l'exploitation forestière, avec ou sans zone tampon, sur les communautés de macroinvertébrés. L'exploitation forestière sans zone tampon a augmenté l'érosion des berges et la sédimentation ultérieure de matériaux des berges a entraîné une augmentation importante de la proportion de particules de sédiments < 9 mm dans le substrat. Bien que l'exploitation forestière ait dégagé le couvert forestier et augmenté la quantité de lumière disponible pour la production primaire, la biomasse des algues n'a pas augmenté après la coupe étant donné que le phosphore est demeuré le facteur limitatif. L'apport de litière allochtone au cours d'eau a diminué de façon importante aux deux sites d'exploitation, mais le site ayant une zone tampon a fourni de plus grandes quantités de litière feuillue au cours d'eau et avait, après la coupe, une population benthique sur pied plus importante que le site sans zone tampon.

Avant et après l'exploitation forestière, les changements saisonniers dans la composition des communautés de macroinvertébrés ont été grandement affectés par le caractère saisonnier de l'écoulement: élevé (hiver), faible (été) et transitoire (printemps et automne). La composition trophique des communautés de macroinvertébrés n'a pas été affectée par l'exploitation forestière, les collecteurs, les collecteurs-râcleurs et les collecteurs-prédateurs dominant en nombre au cours de toutes les saisons et de toutes les années. L'exploitation forestière des berges a entraîné une diminution importante de la densité des macroinvertébrés au cours des hivers, principalement parce que la sédimentation survenue après l'exploitation forestière a augmenté l'affouillement hivernal. Les densités de macroinvertébrés au site sans zone tampon ont également été réduites en été et au cours des périodes de transition à cause de l'intrusion de sédiments dans le substrat et de la formation réduite de détritus. Les communautés de macroinvertébrés ont été touchées moins sévèrement par l'exploitation forestière lorsqu'une zone tampon riveraine d'une largeur < 10 m et des barrages de débris naturels ont été laissés le long du cours d'eau. La zone tampon a réduit l'affouillement lié à l'exploitation forestière au cours de l'hiver, et l'apport de litière feuillue au cours de l'été et de la période de transition ressemblait davantage aux conditions existant avant l'exploitation forestière.

Des manipulations expérimentales de la taille des particules du substrat ainsi que des études sur la qualité et la quantité des débris ont été effectuées sur le terrain et ont établi que la qualité et la quantité des débris étaient plus importantes pour déterminer la distribution et l'abondance

des macroinvertébrés que la taille des particules du substrat. Les réactions aux détritus ont varié entre les taxons de macroinvertébrés et même entre les membre du même groupe trophique.

Des expériences sur l'addition de sédiments ont été effectuées pour déterminer l'effet du mouvement vers l'aval de sédiments fins par saltation sur la dérive des invertébrés et la densité du benthos. La saltation de sédiments a augmenté les taux de dérive et a diminué les densités du benthos, l'époque et le régime des augmentations de dérive étant liés à la distribution verticale de macroinvertébrés dans le substrat.

Vu que les berges des cours d'eau côtiers fournissent des apports importants d'énergie aux communautés de macroinvertébrés et contribuent à l'apport de sédiment au cours d'eau, l'exploitation forestière des berges est nuisible aux macroinvertébrés. Des lignes directrices d'aménagement doivent protéger la zone de contact des berges avec la forêt si l'on veut que les cours d'eau côtiers demeurent un habitat productif pour l'élevage d'alevins de saumon.

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1. INTRODUCTION

1.1 Importance of Coastal Streams

Small coastal streams in British Columbia provide an important rearing habitat for coho salmon (Oncorhynchus kisutch (Walbaum)) since the fry utilize benthic invertebrates as a major food source (Mundie 1971; 1974) during their 1-2 year residency (Anderson 1981). Clearcutting of the forest within the watersheds of these 1st-3rd order (sensu Strahler 1957) salmonid streams has produced significant changes in the lotic environment (Mason and Narver 1975). These environmental perturbations effect all trophic levels of the stream ecosystem, but quantitative ecological studies have primarily been restricted to the documentation of how changes in the abiotic environment (e.g. sedimentation) effect fish production (Gibbons and Salo 1973). Very little attention has been given to quantifying the effects of logging on benthic macroinvertebrate communities of coastal streams in British Columbia, although responses of macroinvertebrates to logging have been investigated in other regions of North America (Tebo 1957; Burns 1972; Newbold, Erman and Roby 1980; Murphy and Hall 1981).

The major impacts of logging operations on macroinvertebrate communities are mediated through shifts in abiotic and biotic environmental components of the stream ecosystem either individually or in unison. The primary abiotic parameters potentially affected by logging are stream discharge, bank stability, sedimentation, insolation, water temperature and the terrestrial release of inorganic nutrients (Gibbons and Salo 1973). The main potential biotic impacts of logging to the stream ecosystem are changes in allochthonous and autochthonous energy inputs which directly or indirectly affect all trophic levels.

1.2 Abiotic Impacts of Logging

In the coastal streams of British Columbia discharge rapidly responds to the high intensity and amount of rainfall in the catchment basin. Organic debris dams (i.e. natural accumulations of large woody debris) function to impede water flow and, therefore, are determinants of channel form (Keller and Swanson 1979), gravel and sediment movement (Swanson, Lienkaemper and Sedell 1976), and the export of organic matter (Bilby and Likens 1980; Bilby 1981). Following forest removal the difference between minimum and maximum discharge is greater (Rothacher 1970), and in Carnation Creek the higher storm discharge may partly account for the decreased number and stability of debris dams after logging (Toews and Moore 1978). The removal of debris dams leads to increased streambank erosion, a general widening of the streambed, and potentially large inputs of fine sediments from the eroding banks. If the higher sediment load is not removed from the stream by the storm hydrograph, the fine

sediments will accumulate and remain in the streambed throughout the low discharge period. Lotic macroinvertebrate populations are detrimentally affected by increased proportions of fine sediment in the substrate (Chutter 1969; Nuttal and Bielby 1973; Rosenberg and Snow 1975; McClelland and Brusven 1980) and high suspended sediment levels (Rosenberg and Wiens 1978a; 1980), so that logging related sedimentation may strongly affect macroinvertebrate communities. Significant amounts of fine sediment input can also result from road construction which has been implicated as a major source of sedimentation in logged watersheds (Fredriksen 1965; Brown and Krygier 1971; Megahan and Kidd 1972).

Canopy removal substantially raises the amount of sunlight reaching the soil surface of the catchment basin which increases soil, groundwater and ultimately stream temperature, particularly in the summer (Gray and Edington 1969; Brown 1971). The loss of the canopy also allows a more rapid and greater heat loss from the stream surface which produces larger diurnal water temperature fluctuations, and lower water temperatures in the winter (Eschner and Larmoyeux 1963; Meehan 1968; Likens, Bormann, Johnson, Fisher and Pierce 1970; Fredriksen 1971). Insect growth rate and fecundity are related to the thermal regime of the stream (Vannote and Sweeney 1980), so logging related water temperature changes may affect macroinvertebrate community structure and composition.

1.3 Biotic Impacts of Logging

The dominant post-logging biotic impacts to a stream are related to substantial shifts in the proportions of allochthonous and autochthonous energy inputs. Low-order streams draining northern temperate forests are known to derive a significant portion of their total energy budget from deciduous and coniferous leaf litter (Fisher and Likens 1973; Vannote, Minshall, Cummins, Sedell and Cushing 1980). These streams typically are strongly heterotrophic, with autochthonous autotrophic production (P) less than the rate of community respiration (R) (i.e. $P/R < 1$). The relative importance of autochthonous autotrophic production increases only if more sunlight reaches the streambed (Minshall 1978). Thus, the macroinvertebrate communities of heavily forested streams, like Carnation Creek, are structured to process particulate detritus (Minshall 1967; Mackay and Kalff 1973; Cummins 1974; Vannote, Minshall, Cummins, Sedell and Cushing 1980). A reduction or cessation of allochthonous input will not only alter a stream's energy budget, but must also alter structure and composition of the macroinvertebrate communities dependent upon it.

Post-logging losses in allochthonous sources of primary production may be partly counterbalanced by higher autochthonous primary production due to post-logging increases in water temperature, photosynthetically available radiation (PAR), and available nutrients (Stockner and Shortreed 1978). However, as

increased nutrient levels may only prevail for up to five years after slash burning (Fredriksen 1971; Gibbons and Salo 1973), algal production will likely return to pre-logging levels after this period (Stockner and Shortreed 1978). Furthermore, the potential for immediate post-logging increases in algal production may be reduced by increased sedimentation, scouring, and turbidity (Hansmann and Phinney 1973).

Due to shifts in proportions of autochthonous and allochthonous energy inputs, the energy budget and trophic structure of logged 1st-3rd order streams should resemble larger 4th-6th order streams if the River Continuum Concept (RCC) proposed by Vannote, Minshall, Cummins, Sedell and Cushing (1980) is valid. The RCC suggests that mid-order streams should have the following characteristics: (1) they should have less coarse particulate (CPOM) (i.e. > 1 mm) than fine particulate organic matter (FPOM) (i.e. < 1 mm) in the substrate; (2) autochthonous autotrophic production should provide a significant food base both directly to grazers, and indirectly to detritivores; and (3) autotrophy should prevail at least during a major portion of the year with P/R > 1. RCC hypthesizes that the abundance of each macroinvertebrate functional feeding group (Cummins 1973; Merritt and Cummins 1978) will directly correspond to the particle size composition of organic matter in the substrate. Decreases in CPOM should therefore reduce the density of shredders while increases in algal production and the overall decrease in detritus particle size should increase collector and collector-scraper densities.

1.4 Objectives

The objectives of the Carnation Creek study are:

1) to investigate the importance of riparian buffer zones to macroinvertebrate communities;

2) to document the seasonal dynamics of pre- and post-logging macroinvertebrate communities;

3) to document the trophic guild structure of pre- and post-logging macroinvertebrate communities;

4) to experimentally determine the relative importance of detritus and substrate composition in macroinvertebrate microdistribution;

5) to determine the short-term effects of experimental increases of fine sediments (< 2 mm) on macroinvertebrate communities; and

6) with reference to the results of objectives 1-5, to indicate the direct and indirect effects of logging on macroinvertebrate communities and their secondary effects on salmonid production.

2. STUDY AREA

2.1 General Description

Carnation Creek is a third-order stream in the Coastal Western Hemlock (Tsuga heterophylla (Bong)) biogeoclimatic zone (Klinka, Nuszdorfer and Skoda 1979), and flows into Barkley Sound on the west coast of Vancouver Island, British Columbia (Figure 1). The stream is 6 km long, and drains a 10 km^2 area. Annual rainfall is 280-350 cm/yr and stream discharge can vary from a summer minimum of .015 m^3/s to a maximum of 42.5 m^3/s during winter storms. Before logging (1971-1974) mean water temperatures in winter (November-March) and summer (June-August) approached 5 and 12 ^{o}C, respectively. Snow accumulations of up to 1 m occasionally occur at the highest point in the watershed (700 m), but are short-lived because of frequent warm, moist Pacific disturbances. Scrivener (1975) has given a detailed description of the water chemistry of Carnation Creek, and Stockner and Shortreed (1976) classify the stream as highly oligotrophic because of the extremely low values of total dissolved solids and plant nutrients (Table 1). Dissolved oxygen remains near saturation even during low summer discharge, while pH annually ranges from 6.0-7.2. A barrier falls prevents anadromous salmon, including coho and chum (Oncorhynchus keta Walbaum)), from reaching the upper 2.8 km of the stream. Thus, the macroinvertebrate study was restricted to the lower 3.2 km of the stream which has an average gradient of 1.9%. The streambed substrate composition of this lower reach is a mixture of sand to cobble particle sizes (sensu Cummins 1962).

The soils within the watershed are primarily composed of shallow, gravel colluvium overlying bedrock of volcanic origin (Oswald 1973; 1974). Prior to logging, the forest consisted of western hemlock, western red cedar (Thuja plicata Donn), amabilis fir (Abies amabilis Forbes) and Sitka spruce (Picea sichensis Bong) (Oswald 1973; 1974) with a a riparian vegetation of red alder (Alnus rubra Bong), salmonberry (Rubus spectabilis Pursh), salal (Gaultheria shallon Pursh), deer fern (Blechnum spicant Roth) and western sword fern (Polystichum minitum (Kaulf.))-(Oswald 1975).

2.2 Detailed Description of Study Sites

Three 100 m long sampling sites (630m, 1480m and Tributary C (TRC); Figure 1) were established with the riparian vegetation, substrate composition and stream gradient similar within each sampling reach. Until October 1976, all three sampling sites were representative of pre-logging conditions as road construction was located far away from the floodplain. The only clearcutting (<2% of watershed) was largely downstream of site 630m and was separated from the stream by a wide (20-50 m) riparian buffer strip. Large areas adjacent to the stream were

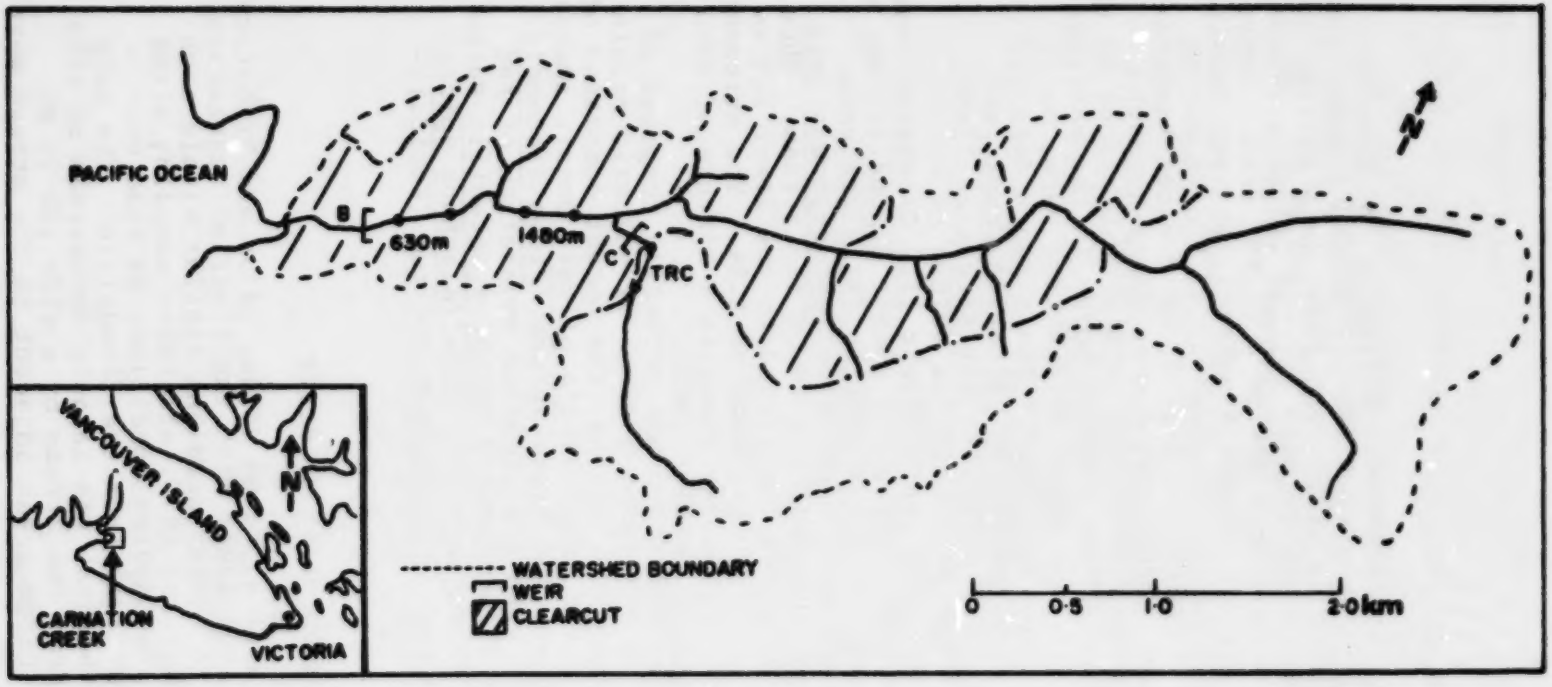

Figure 1. Carnation Creek watershed showing the hydrologic weirs, the clearcutting boundaries and the macroinvertebrate sampling sites. ●——● defines the upper and lower boundaries of each sampling site.

Table 1. Maximum values of total dissolved solids (TDS) and plant nutrients in Carnation Creek, 1974-1975 (from Stockner and Shortreed 1976).

TDS	<25 mg/l
NO_3 - (N)	<2.50µg atoms/l
NH_4 + (N)	<0.30µg atoms/l
Total Phosphorus	<0.05µg atoms/l
SiO_2	<34.0µg atoms/l

clearcut during the fall and winter 1976-77 and 1977-78 so that 27% of the watershed was clearcut by March 1978 (MacMillan Bloedel Limited 1979). By 1977 each of the three sites represented a distinct streamside logging treatment: (1) 630m, a logged stream reach with undisturbed debris dams and an intact 10 m wide riparian vegetation buffer strip; (2) 1480m, a logged stream reach with both debris dams and all riparian vegetation removed; and (3) Tributary C, an unlogged tributary.

A suitable control site could not be established in the unlogged upper 2.8 km of Carnation Creek because (1) the substrate was more coarse than in the lower reach; (2) the upper section was inaccessible to anadromous salmon; and (3) access for sampling was limited by the steep canyon walls. Since all of the forest around lower Carnation Creek was disturbed by logging, site TRC was the only possible control site. Although site TRC was indicative of the annual seasonal variation that occurred in an unlogged stream reach, even during the pre-logging years (1974-76) it had a substantially different discharge regime, scouring pattern and leaf litter input than sites 630m and 1480m. Thus, the only strict control for the logged sites (630m and 1480m) was the three year pre-logging period.

2.3 Discharge Regime 1974-1981

Mean monthly discharge was continuously recorded by Environment Canada over the period 1974-1981. Discharge patterns in Carnation Creek are seasonally predictable and can be categorized into a period of high discharge and frequent spates (November through March) and a low discharge period (June through August) when discharge never exceeded 0.6 m^3/s (Figure 2). During the high discharge period the mean monthly discharge was consistently > 1 m^3/s and with the exceptions of the 1976-77 and 1977-78 periods, exceeded 2 m^3/s for one or more months. The months of April, May, September and October were always transitional to the high and low discharge periods.

2.4 Water Temperature Regime 1974-1981

Water temperature was continuously recorded by Environment Canada at B and C weirs (Figure 1) over the period 1974-1981. Mean monthly water temperature ranged between 1.7-8.4 ^{o}C throughout the high discharge period (November-March) and between 8.4-15.2 ^{o}C during low discharge (June-August) (Appendix I). Since air and water temperatures were warmer throughout the watershed from 1977-81 compared to 1974-76 (Hartman, Anderson and Scrivener 1982) (Appendix I), a site specific comparison of pre- and post-logging values could not be made. However, the impact of logging on water temperature regime can be inferred by comparing the number of degree days per month (i.e. sum of the mean daily water temperatures) accumulated at B and C weirs in 1975 when the forest around both sites was unlogged, compared to 1979 when the soils around B weir were exposed to higher amounts

of sunlight (Figure 3). Chi-square analysis indicates that the 1975 monthly degree day regimes for B and C weirs were not significantly different, but that by 1979 when 33% of the watershed had been clearcut, B weir accumulated a significantly higher number of degree days. Prior to logging the annual degree days at B and C weirs were similar (Figure 4). As a progressively greater percentage of the watershed was clearcut from 1977 (12%) through 1981 (40%), the annual degree day accumulation at B weir was consistently higher than C weir.

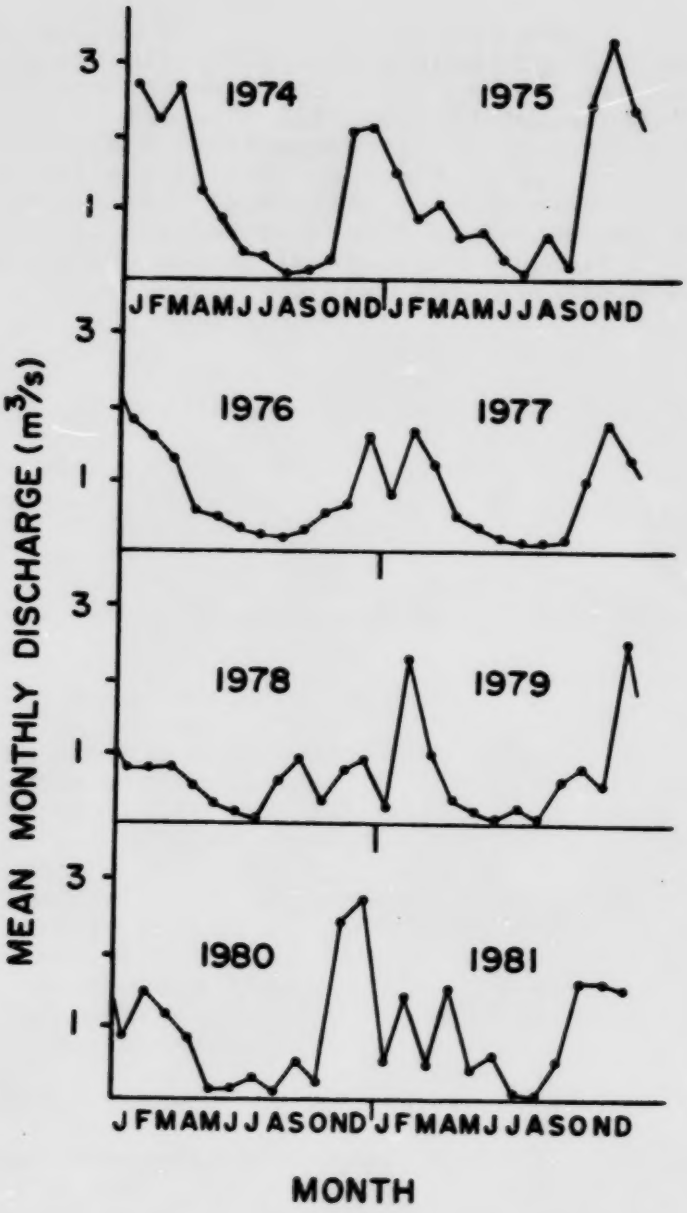

Figure 2. The mean monthly discharge (m^3/s) at B weir over the period January 1974 to December 1981.

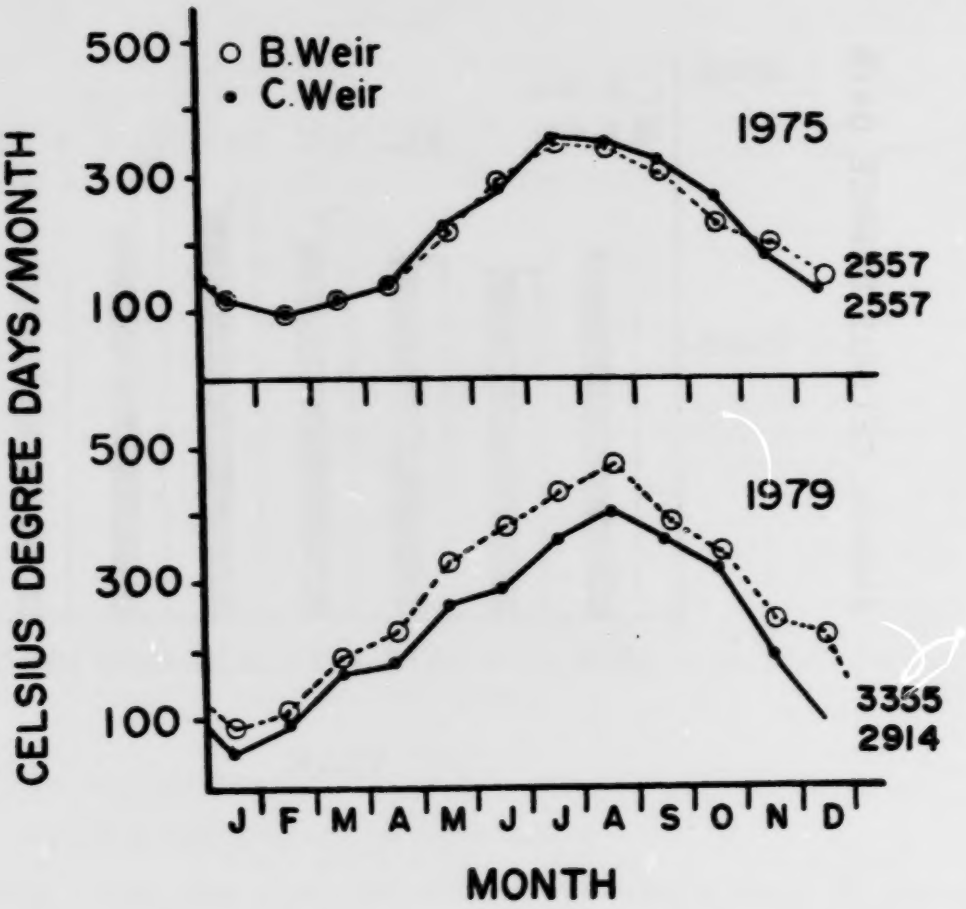

Figure 3. The Celsius degree days accumulated for each month of 1975 and 1979 at B and C weirs. Annual degree day totals are plotted on the right.

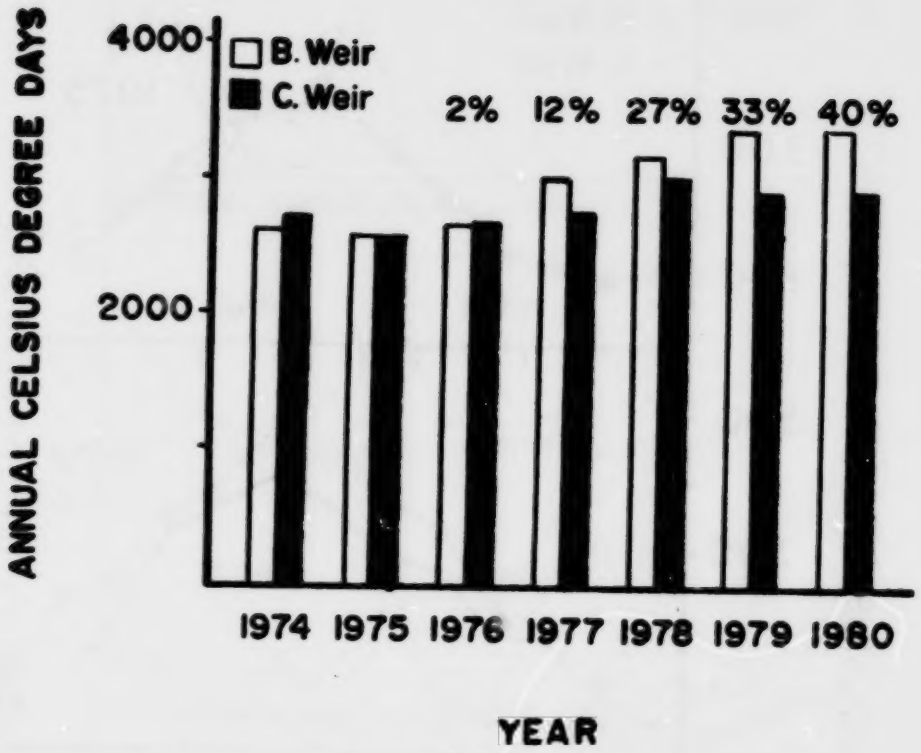

Figure 4. Annual Celsius degree day accumulation at B and C weirs from 1975-1980. The cumulative percentage of the watershed which was clearcut is given for each year.

3. STATISTICAL METHODS

All of the statistics used in Chapters 2, 4 and 5 are described below either under the heading of univariate (one dependent variable) or multivariate (two or more dependent variables) statistics. Hypothesis rejection for all analyses was performed at the $p = 0.05$ level of probability.

3.1 Data Transformation

The appropriate use of parametric statistics (e.g. t-test, analysis of variance, correlation analyses) requires that the sample data meet three criteria (Elliott 1977): (1) the data must be distributed normally; (2) the sample variance should be independent of the mean; and (3) the variance components must be additive. When the sample variance exceeds the mean, as was evident for the benthic macroinvertebrate, detritus, leaf litter and periphyton data, criterion (2) is violated and the original data counts must be normalized. The data from this study were normalized by using the $\log_{10}(x+1)$ (x = original count) transformation (Elliott 1977) before performing a parametric test. Although the fourth-root transformation (Downing 1979) also would have been appropriate, the $\log_{10}$ transformation is most often used by benthic ecologists.

3.2 Univariate Statistics

3.2.1 Testing Differences Between Means

The t-test was used to test the hypothesis that the means of two treatments (groups of samples) were not significantly different (H_o: u1 = u2, two-tailed). This technique is robust to unequal sample sizes, particularly when the two-tailed hypothesis is used (Zar 1974).

When the hypothesis that the differences between the means of three or more treatments were not significantly different (H_o: u1 = u2 = . . . = un) (n = number of treatments), a Model I one-way ANOVA was applied (Zar 1974). If the hypothesis was rejected, Student-Newman-Keuls (SNK) multiple comparison tests (Zar 1974) were used to establish the significantly different means.

3.2.2 Testing Goodness of Fit

The chi-square goodness of fit was used to determine whether the observed frequencies of a variable significantly deviated from the expected frequencies. The Chi-square test is not appropriate when the expected frequencies are less than five, and the Kolmogorov-Smirnov two-sample test (one-tailed) was applied

(Siegel 1956). This one-tailed test determines whether the values of one population are significantly larger than the other (Siegel 1956).

3.3 Multivariate Statistics

3.3.1 Multiple Correlation Analysis

Multiple correlation analysis is appropriate when three or more interrelated variables are investigated and it can not be assumed which variables are functionally dependent upon one another (Zar 1974). Since a significant multiple correlation does not indicate the relative importance of the variables, partial correlations were also calculated. Partial correlation analysis indicates the correlation between each pair of variables while keeping the values of other variables constant (Zar 1974) and, thus, indicates the significant variables of the multiple correlation.

3.3.2 Detrended Correspondence Analysis (DCA)

Indirect ordination methods like DCA reduce the multidimensional species abundance data of quantitative community samples into a graphical illustration of two or three dimensions. The ordination graph represents the relationship between samples based on species composition so that samples with similar composition are plotted close together, and dissimilar samples are far apart. This summarization of the original data can be used as a method for identifying and typifying groups of samples with similar species composition (Nichols 1977).

Detrended correspondence analysis (Hill 1979) is an eigenvector ordination technique based upon reciprocal averaging ordination (RA) which produces a two-dimensional representation for both species and sampling site relationships (Gauch 1982). The first axis of both RA and DCA is determined by arbitrarily assigning each species a score between 0-100, then calculating sample scores by averaging the scores of the species which occur in each sample. The process is repeated, and new species scores are calculated from the scores of the sites containing the species. Through a number of iterations the sample and species scores converge to a unique solution which is not affected by the initial arbitrary species scores (Hill 1973). Subsequent axes can be extracted in a similar manner (Hill 1973, Appendix I).

The main disadvantage of RA ordination has been the "horseshoe appearance" of the second axis which makes the ecological interpretation of this axis difficult (Gauch, Whittaker and Wentworth 1977; Culp and Davies 1980). However, with DCA the second axis is orthogonal and not systematically related to the first axis (Gauch 1982), and describes ecologically meaningful trends in community composition. A second advantage of DCA over RA is that the axes represent standardized

changes in species composition along the axes; the axis units being termed the average standard deviation of species turnover (SD) (Gauch and Whittaker 1972; Gauch 1982). An ordination axis of 1 SD approximately represents a 50% change in community composition (Gauch 1982), and the axis length increases with greater differences in community composition.

DCA was used to determine whether annually recurring seasonal patterns in benthic macroinvertebrate community composition could be established for the sampling sites. However before DCA and other multivariate techniques can be applied, it may be necessary to exclude rare species (< 1% per sample) and to standardize species abundances either through logarithmic or percentage composition transformations (Gauch 1982). As it is not clear which transformation should be applied and whether rare species should always be eliminated, four procedures were used to edit benthic data matrices: (1) $\log_{10}$ transformation; (2) $\log_{10}$ transformation with rare species eliminated; (3) percentage composition transformation; and (4) percentage composition transformation with rare species eliminated. DCA was subsequently applied to each matrix in order to determine the most appropriate procedure. Data transformation to percentage composition with rare species excluded provided the best summarization because most of the variance in seasonal composition was explained by the first axis, and was subsequently used in all ordination analyses.

4. MACROINVERTEBRATE ANALYSES 1974-1980

4.1 Introduction

Inorganic sedimentation was the first documented effect of logging on macroinvertebrate communities (Tebo 1957; Burns 1972) and often is assumed to be the major logging impact, particularly on the benthos of low gradient (< 4%) streams like Carnation Creek, where fine sediments tend to accumulate during periods of low discharge rather than being transported downstream (Murphy and Hall 1981). Although sedimentation often is the only effect of logging considered, of potentially equal or greater importance to the benthic communities are the effects of post-logging changes in allochthonous and autochthonous inputs, and shifts in the water temperature regime (Chapter 1).

The extent to which logging causes environmental changes that detrimentally affect lotic macroinvertebrate communities may be ameliorated by the incorporation of a forest buffer zone along the stream. A buffer zone stabilizes the streambanks and debris dams, and also provides allochthonous leaf litter input. Studies to determine the effects of different streamside treatments, such as clearcutting to the streambank or leaving riparian buffer zones, on macroinvertebrates have only recently appeared in the literature (Newbold, Erman and Roby 1980; Murphy and Hall 1981). These studies suggest that when logging increases the canopy opening, the resulting higher amount of sunlight causes increased autochthonous primary production and thus, higher macroinvertebrate densities. Despite the tendency for macroinvertebrate densities to increase after logging, many studies have shown densities at a logged site equivalent to or lower than at the control site (Newbold, Erman and Roby 1980; Murphy and Hall 1981). However, a fundamental deficiency of all these studies has been the assumption that observed differences between sampling sites are attributable solely to logging. Clearly, normal seasonal variation in community composition, distribution and abundance, and the importance of recent environmental events (e.g. spates, scouring, allochthonous input, etc.) must also be considered.

The study of the responses of Carnation Creek macroinvertebrates to forest removal is based on an intensive before-after experimental design (Hall, Murphy and Aho 1978) which not only includes a post-logging site comparison, but also a site-specific evaluation of pre- and post-logging communities. By investigating the changes in macroinvertebrate density and composition which occur during the seven year pre- and post-logging period, this design enables trends in community composition resulting from logging impacts to be distinguished from those caused by natural seasonal and annual variations.

4.2 Methods

4.2.1 Macroinvertebrate Field and Laboratory Methods

Macroinvertebrate samples from three sampling sites (Section 2.2) were collected monthly from May-September and every 2 months from October-April during the period 1974 through 1980 inclusive. Each sampling site was a riffle composed of gravel, pebble and cobble, and all samples were taken with a modified Neil (1937) cylinder (250 µm mesh) to a standard depth of 10 cm into the substrate. Two replicate samples of 0.1 m^2 were collected prior to July 1979, while 4-8 replicate samples of 0.03 m^2 were collected thereafter. Invertebrates and detritus were separated from the inorganic material in the field by swirling the sample in a pail of water and decanting the suspended organic material into a 106 µm mesh sieve. Samples were preserved in 5-10% formalin. Regular searches of the inorganic material under 12x magnification revealed that fewer than 1% of the total number of animals remained. During 1980, current velocity 2.5 cm above the substrate of each sampling site was measured with a Pygmy Gurley current meter.

From 1974 through 1977 inclusive, macroinvertebrates were hand-sorted from the organic detritus under 12x magnification and identified to species when possible. After 1977, the samples were split into fine (< 1 mm), and coarse (> 1 mm) fractions, and the fine fraction sub-sampled following the technique and protocol of Wrona, Culp and Davies (1982). Five sub-samples of the fine fractions and the entire coarse fraction were sorted and the invertebrates identified to species when possible. After removal of the macroinvertebrates, the fine and coarse detrital fractions were dried at 60 ^{o}C for 48 h, ashed at 500 ^{o}C for 24 h, and the ash-free dry weight of the fractions determined.

4.2.2 Substrate Composition Methods

Two replicate samples were collected from each of the three sampling sites in March, June and November 1980, and January 1981 by imbedding a metal cylinder (.02 m^2) 10 cm into the substrate and removing the contained material. Since the upper lip of the container was above the water level, particles as small as 106 um were quantitatively sampled without loss to the surrounding water. The substrate was dried at 100 ^{o}C for 12 h, divided into eight discreet size classes (phi -5 to phi +2) on the modified Wentworth scale (Cummins 1962), and the percentage composition of each size class determined. Substrate samples were also collected by Environment Canada at sites 630m and 1480m from 1973-1980 (Scrivener and Brownlee 1980).

4.2.3 Leaf Litter Methods

Leaf litter was sampled at each sampling site by placing five 50 x 50 x 10 cm wooden containers with perforated (<500 µm) polyethylene bases under the riparian vegetation approximately

1 m from the streambank. As observations of the traps during high winds (20-80 km/hr) confirmed the effectiveness of leaf litter retention, the traps were emptied at monthly intervals from 1 May to 1 October 1980, and every 2 months from 1 October 1980 to 1 May 1981. The litter was divided into deciduous and coniferous components, dried at 60 ^{o}C for 48 h, and the dry weights determined.

4.2.4 Periphyton Biomass Methods

At the 630m and 1450m sampling sites, periphyton biomass was determined monthly from 1974 to 1979 by Environment Canada (Stockner and Shortreed 1976). Algal biomass was measured by scraping the monthly accumulation of periphyton from plexiglass plates (31 x 31cm) attached to 50 kg concrete blocks. Each periphyton sample was filtered onto a 5.5 cm Whatman glass fiber filter along with 1 ml of saturated $MgCO_3$ to prevent acidification. The filters were macerated before chlorophyll extraction (Yentsch and Menzel 1963), and chlorophyll a calculated according to the equation of Strickland and Parsons (1968).

4.3 Results

4.3.1 1980 Seasonal Patterns of Species Composition

DCA ordination was applied to the 1980 benthic data to establish whether the species composition at the three sampling sites showed consistent seasonal patterns. This year was most appropriate for detailed analysis of seasonality because of the larger number of monthly replicates taken (4-8 per site) than during other years, and the identification of the Chironomidae to genus.

A primary objective of ordination analysis is to reduce sample and species relationships to a low-dimensional space, and appropriate data editing should improve this summarization (Gauch 1982). The DCA ordinations of the 1980 site 630m benthic data showed that all the editing procedures produced similar trends. The January, March and November samples were clustered at one end of the first axis, and the June, July and August samples were positioned at the opposite end, with the remaining months falling between these groups (Figure 5a). Although 94-99% of the variance in species composition was explained by each ordination, the DCA plots of the data transformed to percentage composition provided better summarization because 83-89% of the variance was explained in the first axis, compared to only 57-70% when the $\log_{10}$ transformation was used. The choice between percentage composition including or excluding rare species is arbitrary since the trends and variance explained by each procedure are similar. However, as the omission of rare species simplifies data processing and analysis, this procedure was used in all DCA ordinations of the benthic data.

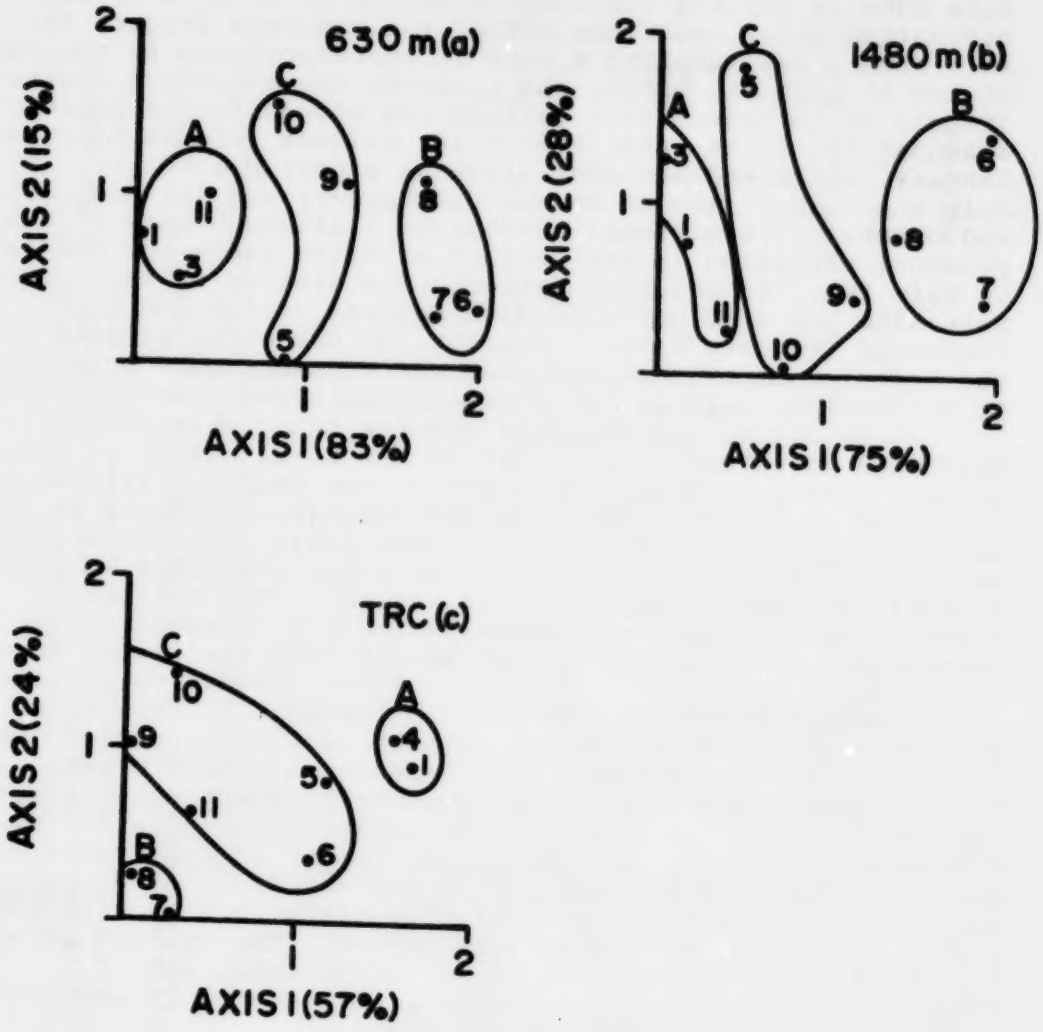

Figure 5. DCA ordinations of the 1980 sites: (a) 630m, (b) 1480m, and (c) TRC. The winter (A), summer (B) and transitional (C) periods are circled, and the variance explained by each axis is given. Each month has been numerically coded from 1 (January) to 12 (December).

The seasonal relationship of benthic species composition at site 630m is largely represented by the first axis of the ordination which describes 83% of the variance (Figure 5a). This axis orders the sampling months in correspondence to the periods of low to high discharge, and by using the discharge regime (Figure 2) to objectively delimit the boundaries of benthic seasonality, three associations are evident (Figure 5a): (A) January, March and November (high or winter discharge); (B) June, July and August (low or summer discharge); and (C) May, September and October (transitional discharge). Although more of the seasonal variation in the benthos at sites 1480m and TRC is shown on axis two, the seasonal patterns are similar to those shown at site 630m and also coincide with periods of low and high discharge (Figures 5a-c). However, at the unlogged site (TRC) the benthic compositions of June and November were more similar to the benthos composition of the transitional period (group C).

To summarize the seasonal changes in benthic composition, only taxa which comprised = 10% of the total number of individuals during at least one month at one sampling site were tabulated (Table 2). The combined relative abundance of these seven taxa always exceeded 45% of the total benthos, and the marked seasonal changes in their relative abundance were diagnostic for the three discharge periods. The horizontal ordering of the sampling months in Table 2 is based on the first ordination axis (Figure 5a), while the taxa are listed according to the first axis scores for the species ordination of site 630m.

Seasonal trends of the benthic communities from sites 630m and 1480m were highly similar with the following periods of high relative abundance evident for the seven diagnostic taxa (Table 2): C. ramaleyi during low discharge; Paraleptophlebia and P. (Polypedilum) in the transitional period; Alloperla during high discharge; and C. reticulata and E. (Iron) in the transitional and high discharge periods. Relative abundance of B. tricaudatus was high throughout the year at site 1480m, but at site 630m peaked during the high discharge period. The benthos at site TRC had similar trends for four of the seven taxa, but Paraleptophlebia, E. (Iron), and B. tricaudatus showed no seasonal trend in relative abundance.

4.3.2 Seasonality of Species Composition at the Sampling Sites During 1974-1979

Ordinations of benthic composition for each site and year were produced, but as the seasonal trends for each site and year were similar, the ordinations for site 1480m are presented (Figures 6a-f) as representative of all sites. Throughout the 1977-1980 post-logging period, seasonal variation in benthic composition at all sampling sites was largely described by axis 1, and benthic seasonality corresponded to the periods of low and high discharge (Figures 5a and 6fd-f). During the pre-logging period, benthic seasonality was more difficult to detect because only four of the diagnostic taxa (Alloperla, B. tricaudatus, Epeorus, Paraleptophlebia) were identified. However, in 1975 the

Table 2. Percentage composition of the seven taxa which represented ≥ 10% of the benthos at the sites during at least one month of 1980. The sampling months and taxa are ordered according to the first axis scores of the 630m DCA ordination.

	High Winter Discharge			Transitional			Low Summer Discharge		
	1-17	3-02	11-13	10-9	5-04	9-18	8-17	7-13	6-18
630m									
Cinygmula ramaleyi	-	-	-	-	1.4	3.5	13.3	26.9	30.8
Paraleptophlebia	-	-	-	11.0	1.4	11.1	6.1	1.1	3.9
Polypedilum Polypedilum	1.4	-	4.4	10.4	2.9	4.8	8.0	3.2	2.4
Cinygmula reticulata	9.0	21.9	16.2	19.6	15.9	38.2	15.5	3.9	8.8
Epeorus Iron	1.4	8.4	-	-	23.5	-	-	1.1	3.8
Alloperla	24.8	20.1	19.1	7.3	11.7	3.7	4.8	10.5	10.9
Baetis tricaudatus	30.2	19.1	40.7	15.5	12.9	10.3	11.0	17.3	1.7
1480m									
Cinygmula ramaleyi	-	-	-	-	-	2.0	7.7	29.7	35.7
Paraleptophlebia	-	-	2.6	6.6	-	13.3	11.5	-	-
Polypedilum Polypedilum	1.5	1.0	-	11.8	3.8	1.6	3.5	2.6	4.2
Cinygmula reticulata	24.1	20.3	16.1	6.7	14.1	15.0	11.7	-	3.3
Epeorus Iron	6.8	14.9	1.4	-	28.8	-	-	1.1	4.5
Alloperla	19.5	22.1	8.0	3.1	10.7	-	2.1	-	3.7
Baetis tricaudatus	31.7	19.2	50.8	55.6	9.6	42.0	20.7	32.7	5.1

-continued-

Table 2. - continued

	High Winter Discharge			Transitional			Low Summer Discharge		
	1-17	3-02	11-13	10-9	5-04	9-18	8-17	7-13	6-18
TRC									
Cinygmula ramaleyi	-	-	-	-	1.9	2.6	4.7	10.0	7.5
Paraleptophlebia	5.3	2.2	-	2.9	2.2	1.8	2.3	3.8	5.1
Polypedilum Polypedilum	-	2.6	-	3.2	4.5	.68	1.9	3.1	2.3
Cinygmula reticulata	10.3	5.4	21.2	15.4	6.0	15.3	7.7	5.8	4.6
Epeorus Iron	3.4	17.3	5.3	1.3	22.6	2.1	1.4	3.0	17.6
Alloperla	15.3	10.8	15.8	14.8	8.3	12.8	9.4	12.0	13.6
Baetis tricaudatus	5.1	7.9	7.3	11.5	5.5	5.1	15.6	12.5	6.9

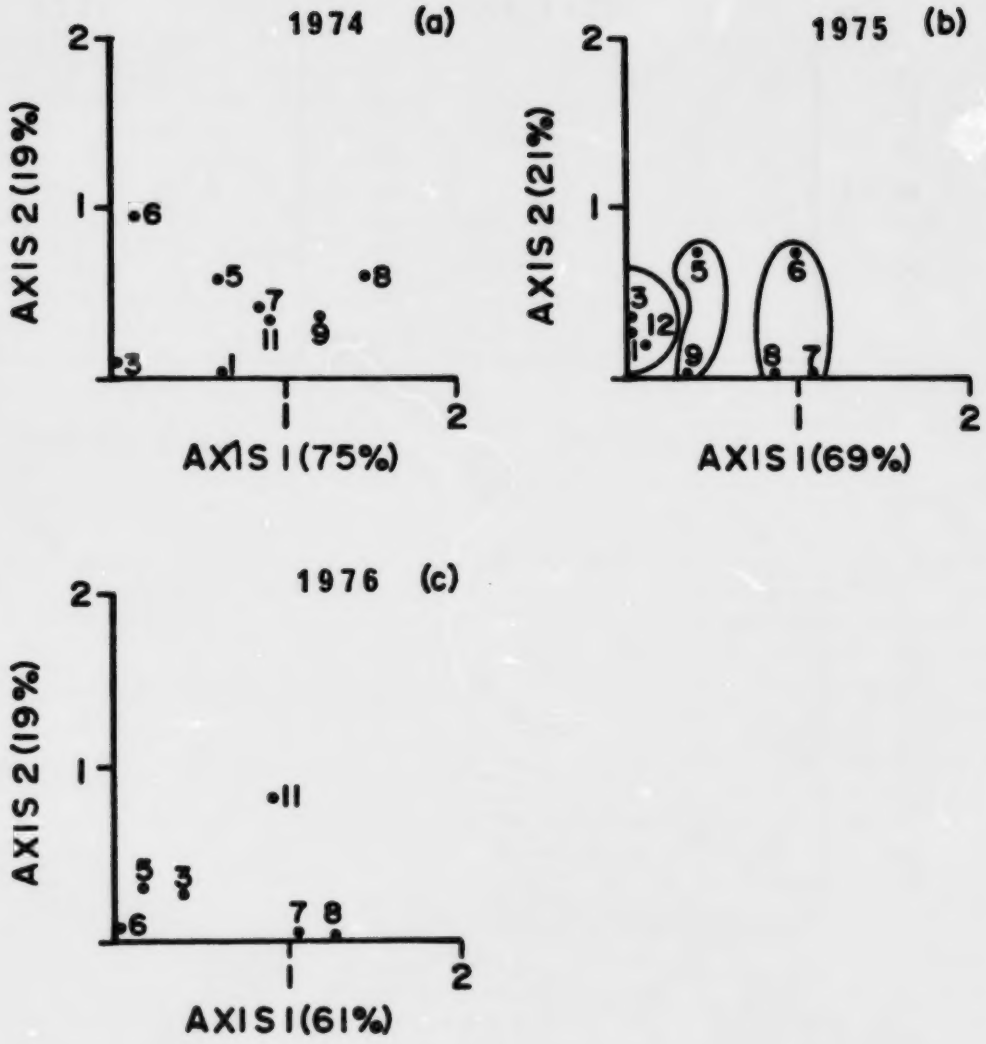

Figure 6. DCA ordinations for site 1480m for the pre- and post-logging years: (a) 1974; (b) 1975; (c) 1976; (d) 1977; (e) 1978; and (f) 1979. The seasonal periods are circled, and the variance explained by each axis is given. Each month has been numerically coded from 1 (January) to 12 (December).

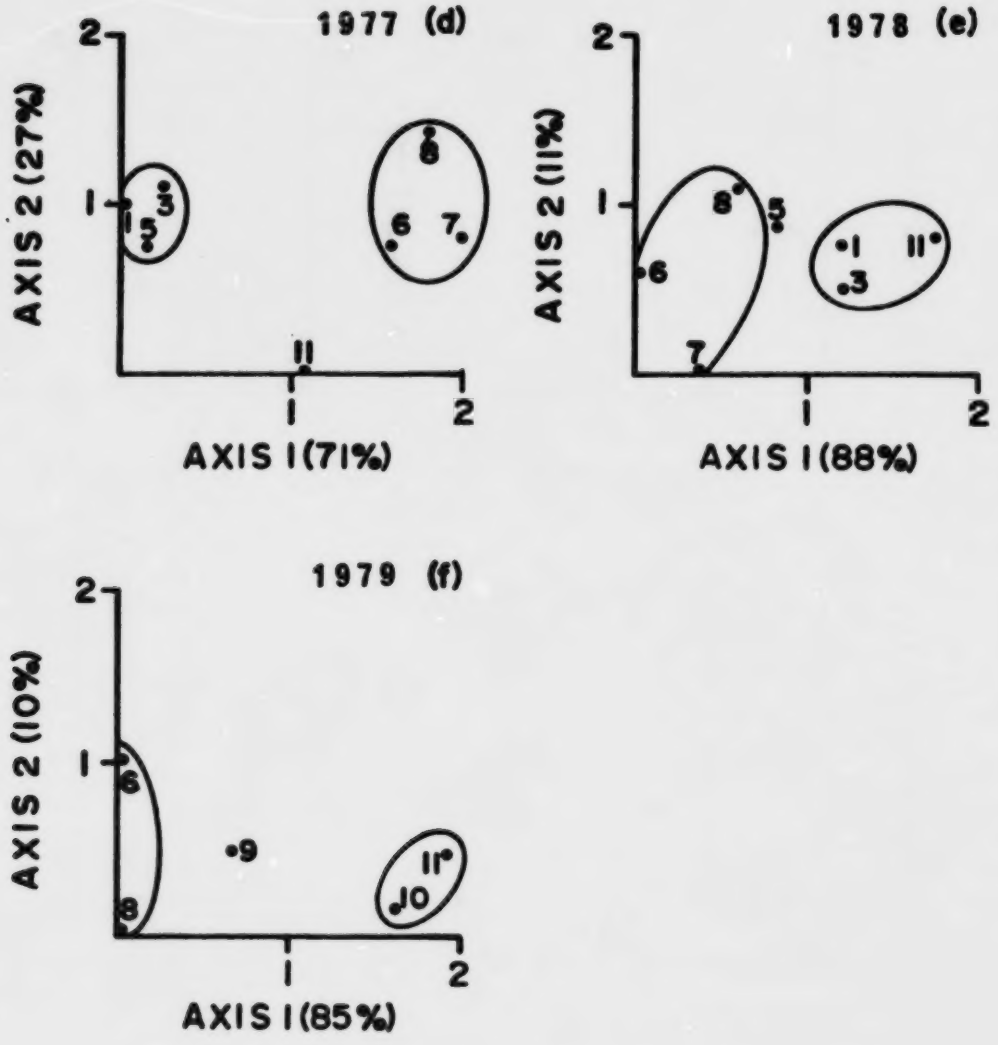

Figure 6. - cont'd.

seasonal variation in the densities of these four diagnostic taxa indicated that the seasonal trends in benthic composition also corresponded to the periods of low and high discharge, and was thus similar to the seasonality observed from 1977-1980.

4.3.3 Annual Density Fluctuations of the Diagnostic Taxa at Each Site for 1974-1980

The seasonal patterns of benthic community composition established by ordination analysis provided an ecologically meaningful structure for further data analyses. Using this seasonal structure, summer (low), transitional and winter (high) discharge period densities of selected taxa were compared with an ANOVA to determine whether between 1974-1980 significant annual variation occurred at sites 630m, 1480m and TRC. This comparison also determined whether the variation in benthic densities at each site changed after logging, and if annual density fluctuations were similar at all three sites. As density comparisons could only be made for taxonomic categories recognized throughout the pre- and post-logging period, the seven diagnostic genera used for the 1980 analysis were contracted to the following six taxa: Alloperla, B. tricaudatus, Chironomidae, Cinygmula, Epeorus (Iron) and Paraleptophlebia. In addition, yearly changes in the densities of the four most abundant shredder detritivores (Capnia, Kathroperla perdita, Leuctra, Nemoura) were tested for significant variation between years, as their densities would likely be affected by reductions in allochthonous input. In these analyses the mean seasonal densities recorded in the pre-logging period (1974-1976) for the above ten taxa were the only valid control comparisons for the post-logging sites with (630m) or without (1480m) a riparian buffer zone.

Between 1974-1980, significant variations in the densities of the diagnostic taxa were recorded at all three sampling sites for the summer, transitional and winter periods (Table 3; Appendices III-XI). As the ranges of year-to-year fluctuations of densities in the summer, transitional and winter periods were similar during both the pre- and post-logging years (Appendices III-XI), mean pre- and post-logging densities for each taxon were calculated for each season, and subsequently compared with a t-test.

A t-test comparison of the pre- and post-logging means established that densities of seven taxa in the summer, and five taxa in each of the transitional and winter periods were lower after logging at the site without a buffer strip (site 1480m) (Tables 4-6). Only the densities of Alloperla, Chironomidae, K. perdita and Leuctra at site 1480m were decreased in all three seasonal periods after logging. The total density of the ten diagnostic taxa was reduced by 41% in the winter and 50% in the summer and transitional periods, compared to the three pre-logging seasons.

Table 3. Results of ANOVA tests which for each site determined significant differences in the yearly mean density of the common taxa found during the summer, transitional and winter periods. (+ = significant; ns = not significant)

	Summer			Transitional			Winter		
	630	1480	TRC	630	1480	TRC	630	1480	TRC
Alloperla	+	+	ns	+	+	+	+	+	+
B. tricaudatus	+	+	+	ns	ns	+	+	+	+
Capnia	ns	+	ns	ns	ns	ns	ns	ns	ns
Chironomidae	ns	+	+	ns	+	+	ns	+	ns
Cinygmula	+	+	+	ns	ns	ns	+	+	+
Epeorus	+	+	ns	ns	ns	ns	ns	ns	ns
K. perdita	+	+	+	+	+	+	+	+	+
Leuctra	ns	+	+	ns	+	ns	+	+	+
Nemoura	+	+	+	ns	+	ns	ns	+	ns
Paraleptophlebia	+	ns	+	ns	ns	ns	+	+	+

Table 4. Individual mean density (no./0.1m^2) and standard error, and total density of the diagnostic taxa in the summer pre- and post-logging periods. (* indicates a significant difference between pre- and post-logging values).

Taxa	630m		1480m		TRC	
	Pre	Post	Pre	Post	Pre	Post
Alloperla	*198 ± 29	*108 ± 16	*211 ± 25	* 35 ± 6	115 ± 16	80 ± 17
B. tricaudatus	*155 ± 38	* 75 ± 12	*193 ± 40	*114 ± 28	* 31 ± 6	* 85 ± 13
Capnia	10 ± 4	5 ± 1	* 10 ± 4	* 5 ± 2	1 ± 1	2 ± 1
Chironomidae	253 ± 47	195 ± 21	*317 ± 70	*149 ± 16	183 ± 31	173 ± 44
Cinygmula	142 ± 22	224 ± 21	158 ± 21	153 ± 16	92 ± 13	75 ± 9
Epeorus	* 68 ± 17	* 15 ± 5	* 80 ± 16	* 16 ± 3	25 ± 10	32 ± 7
K. perdita	* 6 ± 2	* 3 ± 1	* 6 ± 2	* 1 ± 1	6 ± 1	10 ± 2
Leuctra	11 ± 2	13 ± 3	* 8 ± 2	* 1 ± 1	16 ± 5	11 ± 2
Nemoura	14 ± 3	8 ± 1	34 ± 9	20 ± 4	11 ± 4	15 ± 2
Paraleptophlebia	42 ± 12	61 ± 11	43 ± 8	35 ± 8	17 ± 4	20 ± 2
Total Density	* 899	* 707	* 1060	* 529	497	503

Table 5. Individual mean density (no./0.1m^2) and standard error, and total density of the diagnostic taxa in the transitional pre- and post-logging periods. (* indicates a significant difference between pre- and post-logging values).

Taxa	630m		1480m		TRC	
	Pre	Post	Pre	Post	Pre	Post
Alloperla	*224 ± 33	*124 ± 15	*227 ± 27	* 45 ± 5	*159 ± 23	* 78 ± 8
B. tricaudatus	* 81 ± 22	*139 ± 16	105 ± 26	239 ± 75	42 ± 14	36 ± 6
Capnia	24 ± 10	20 ± 7	37 ± 20	11 ± 4	2 ± 1	4 ± 1
Chironomidae	310 ± 68	189 ± 36	*543 ± 217	*130 ± 28	*342 ± 82	* 69 ± 11
Cinygmula	258 ± 67	327 ± 60	246 ± 71	137 ± 22	117 ± 32	86 ± 17
Epeorus	61 ± 23	57 ± 18	78 ± 26	45 ± 14	117 ± 42	54 ± 10
K. perdita	7 ± 3	2 ± 1	* 7 ± 3	* 1 ± 1	11 ± 3	10 ± 2
Leuctra	17 ± 5	15 ± 5	* 21 ± 8	* 2 ± 1	30 ± 8	24 ± 4
Nemoura	5 ± 1	7 ± 2	* 7 ± 3	* 3 ± 1	10 ± 3	6 ± 2
Paraleptophlebia	* 23 ± 5	* 85 ± 19	75 ± 30	62 ± 19	25 ± 6	14 ± 2
Total Density	1010	965	* 1346	* 675	* 855	* 381

Table 6. Individual mean density (no./0.1m^2) and standard error, and total density of the diagnostic taxa in the winter pre- and post-logging periods. (* indicates a significant difference between pre- and post-logging values).

Taxa	630m		1480m		TRC	
	Pre	Post	Pre	Post	Pre	Post
Alloperla	128 ± 21	91 ± 8	*144 ± 12	* 40 ± 9	134 ± 23	75 ± 8
B. tricaudatus	* 31 ± 6	* 95 ± 10	50 ± 11	112 ± 28	14 ± 6	29 ± 9
Capnia	7 ± 3	8 ± 2	5 ± 3	6 ± 1	2 ± 1	5 ± 2
Chironomidae	162 ± 44	85 ± 18	*207 ± 44	* 95 ± 48	*164 ± 29	*56 ± 11
Cinygmula	*140 ± 23	* 82 ± 14	*133 ± 23	* 67 ± 19	68 ± 11	66 ± 9
Epeorus	5 ± 1	11 ± 3	23 ± 8	18 ± 8	43 ± 14	24 ± 5
K. perdita	* 4 ± 1	* 1 ± 1	* 7 ± 1	* 1 ± 1	6 ± 3	12 ± 5
Leuctra	* 16 ± 3	* 3 ± 1	* 13 ± 3	* 3 ± 1	21 ± 5	12 ± 4
Nemoura	* 5 ± 1	* 1 ± 1	2 ± 1	1 ± 1	4 ± 1	5 ± 1
Paraleptophlebia	9 ± 3	9 ± 2	22 ± 5	13 ± 6	10 ± 1	10 ± 2
Total Density	*507	*386	*606	*356	*466	*294

With a riparian buffer strip present, the post-logging reductions in total density of the diagnostic taxa at site 630m only ranged from 21-24% in the summer and winter, with no difference observed in total density for the transitional period (Tables 4-6). A maximum of four taxa showed post-logging density decreases at site 630m (Tables 4 and 6), and only Alloperla and K. perdita were reduced in more than one seasonal period (Tables 4-6). While a post-logging increase in density was never observed at site 1480m, at site 630m, B. tricaudatus showed significant increases in the transitional and winter periods (Tables 5 and 6), and Paraleptophlebia increased in the transitional period (Table 5). Thus, logging appeared to have a greater detrimental effect on macroinvertebrate density in the stream reach without a buffer strip.

At the unlogged site (TRC), the mean densities of only three diagnostic taxa were significantly different over the 1974-1976 period, compared to 1977-1980 (Tables 4-6). During the winter periods 1977-1980, Chironomidae densities were lower than in the comparable seasons in 1974-1976 (Table 6). Similarly, for the 1977-1980 transitional periods, densities of both Alloperla and Chironomidae were lower than in 1974-1976 (Table 5). These density decreases were reflected in the lower total densities of the 1977-1980 transitional and winter periods (Tables 5 and 6). Although the summer densities of B. tricaudatus for 1977-1980 were higher than for 1974-1976, total densities of both summer periods were similar (Table 4).

4.3.4 Site-to-Site Comparison of Pre- and Post-Logging Benthic Densities

The lack of a good post-logging control site was overcome by using ANOVA analyses to determine whether, relative to one another, the three sampling sites showed consistent density trends during the three pre-logging years. If a recurring density relationship among the sites could be established for the pre-logging period, a post-logging change in this pattern could be attributed to the effects of logging since site TRC remained unlogged. This analysis required the calculation of 30 ANOVA's per year (ten for each seasonal period), which are summarized into pre- and post-logging years (Table 7).

Throughout the pre-logging period, site TRC had significantly lower summer densities of B. tricaudatus, Capnia, Chironomidae, Epeorus, Nemoura and Paraleptophlebia compared with sites 630m and 1480m, while Alloperla, Cinygmula, K. perdita and Leuctra densities were never significantly different between the sites (Tables 4 and 7). In the summers following logging, five of the ten diagnostic taxa showed a different pattern, with the lowest densities of Alloperla, Chironomidae, K. perdita and Leuctra at site 1480m, without a buffer zone, and Epeorus densities at sites 630m and 1480m were significantly lower than at site TRC.

Table. 7 Pre- and post-logging summarization of ANOVA tests which determined significant differences in density between the sites during the summer, transitional and winter periods of each year.
(+ = significant; ns = not significant)

	Summer		Transitional		Winter	
	Pre	Post	Pre	Post	Pre	Post
Alloperla	ns	+	+	+	+	+
B. tricaudatus	+	+	+	+	+	+
Capnia	+	ns	ns	+	ns	ns
Chironomidae	+	+	ns	+	ns	+
Cinygmula	ns	+	ns	+	+	+
Epeorus	+	+	ns	ns	ns	+
K. perdita	ns	+	ns	+	ns	+
Leuctra	+	+	ns	+	ns	+
Nemoura	+	ns	ns	ns	ns	+
Paraleptophlebia	+	+	ns	+	ns	+

Throughout the transitional discharge period, the pre-logging densities of most taxa at sites 630m, 1480m and TRC were not significantly different (Table 7). For the first two years after logging (1977-1978), the only significant change from this pre-logging trend was the reduction in Alloperla density at site 1480m, compared to its densities at sites TRC and 630m (Appendices VI-VIII). However, by 1980 the density of two shredders, K. perdita and Leuctra, had also decreased at site 1480m, and Paraleptophlebia densities had increased at both logged sites (630m and 1480m) (Appendices VI and VII).

In the winters of the pre-logging years, densities of most taxa were not significantly different between sampling sites (Table 7). No change occurred in the first winter after logging, but in the second (1978) and subsequent post-logging winters, significantly lower densities of Alloperla, Chironomidae, Epeorus and Paraleptophlebia were recorded at site 1480m, and Leuctra densities at both logged sites were reduced compared to the unlogged site (Appendices IX-XI). In 1980 the densities of K. perdita at the logged sites were significantly lower than at site TRC, and Cinygmula density was lowest at site 1480m (Appendices IX-XI).

4.3.5 Annual Fluctuation of Trophic Guild Density at Each Site for 1974 to 1980

All macroinvertebrates were categorized into trophic guilds (functional feeding groups) following Merritt and Cummins (1978), and Hawkins and Sedell (1981), except for Alloperla species, which in Carnation Creek are collector-predators (Scrivener unpublished data). Although seven trophic guilds occur in Carnation Creek, two (filter-feeders and predators) were omitted from the analyses because they were rare (< 1% per sample). The remaining five guilds were compared seasonally.

A one-way ANOVA indicated that from 1974-1980 most trophic guilds exhibited significant year-to-year fluctuations in density at each sampling site during each of the three seasons (Table 8). However, as the density fluctuations of the pre- and post-logging periods were of a similar magnitude, mean pre- and post-logging densities for each trophic guild were calculated. T-test comparisons of the pre- and post-logging means at site 1480m indicate that depending on the season, from 3-5 trophic guilds decreased in density after logging (Tables 9-11). Post-logging densities of collector-scrapers and collector-predators at site 1480m were significantly decreased in all seasons, while collectors decreased in the summer and transitional periods, and the shredders decreased in the transitional and winter. In contrast, at site 630m with a buffer zone, the only significantly lower post-logging densities were recorded for collector-predators in

Table 8. Results of ANOVA tests which for each site determined significant differences in the yearly mean density of the common trophic guilds found during the summer, transitional and winter periods.
(+ = significant; ns = not significant)

	Summer			Transitional			Winter		
	630	1480	TRC	630	1480	TRC	630	1480	TRC
Collector	ns	+	+	ns	ns	+	+	+	+
Collector-Scraper	+	+	+	+	+	+	+	+	ns
Collector-Predator	+	+	ns	+	+	+	+	+	ns
Scraper	ns	+	+	ns	ns	ns	ns	+	ns
Shredder	ns	+	ns	ns	+	ns	+	+	ns

Table 9. Mean trophic guild densities (no./0.1m^2) and the standard error for the summer pre- and post-logging periods. (* indicates a significant difference between pre- and post-logging values.)

	630m		1480m		TRC	
Trophic Guild	Pre	Post	Pre	Post	Pre	Post
Collector	523 ± 80	400 ± 39	*647 ± 100	*366 ± 45	328 ± 46	345 ± 56
Collector-Scraper	225 ± 37	240 ± 21	*263 ± 34	*174 ± 17	134 ± 21	108 ± 11
Collector-Predator	*198 ± 29	*108 ± 15	*211 ± 25	* 35 ± 6	*115 ± 16	* 80 ± 7
Scraper	21 ± 15	21 ± 9	6 ± 3	1 ± 1	* 8 ± 4	* 75 ± 25
Shredder	47 ± 8	43 ± 7	70 ± 11	27 ± 5	43 ± 8	54 ± 9

Table 10. Mean trophic guild densities (no./0.1m^2) and the standard error for the transitional pre- and post-logging periods. (* indicates a significant difference between pre- and post-logging values.)

	630m		1480m		TRC	
Trophic Guild	Pre	Post	Pre	Post	Pre	Post
Collector	538 ± 77	510 ± 52	*846 ± 278	*488 ± 104	*614 ± 113	*222 ± 23
Collector-Scraper	362 ± 87	385 ± 54	*420 ± 118	*188 ± 21	*337 ± 55	*150 ± 16
Collector-Predator	*224 ± 33	*124 ± 15	*227 ± 27	* 45 ± 5	*159 ± 23	* 79 ± 9
Scraper	4 ± 2	6 ± 2	* 6 ± 4	* 1 ± 1	29 ± 15	33 ± 9
Shredder	56 ± 16	52 ± 12	* 75 ± 27	* 17 ± 5	55 ± 13	60 ± 13

Table 11. Mean trophic guild densities (no./0.1m^2) and the standard error for the winter pre- and post-logging periods. (* indicates a significant difference between pre- and post-logging values.)

	630m		1480m		TRC	
Trophic Guild	Pre	Post	Pre	Post	Pre	Post
Collector	276 ± 55	254 ± 32	385 ± 59	258 ± 88	*378 ± 88	*172 ± 27
Collector-Scraper	*157 ± 23	*101 ± 16	*177 ± 28	* 88 ± 27	*212 ± 50	*101 ± 10
Collector-Predator	128 ± 21	91 ± 8	*144 ± 12	* 40 ± 9	*134 ± 23	* 75 ± 8
Scraper	1 ± 1	1 ± 1	* 8 ± 4	* 1 ± 1	* 8 ± 2	* 24 ± 6
Shredder	* 29 ± 6	* 13 ± 3	* 25 ± 6	* 9 ± 2	32 ± 5	31 ± 4

the summer and transitional periods, and for collector-scrapers and shredders in the winter (Tables 9-11). At the unlogged site (TRC), densities of 1-3 trophic guilds were lower during 1977-1980 (Tables 9-11). Although from 1977-1980, densities at the logged sites were never higher than the 1974-1976 densities, at site TRC the 1977-1980 summer and winter densities of scrapers were significantly higher than 1974-1976 densities (Tables 9 and 11).

The post-logging densities of several trophic guilds decreased from the pre-logging values, particularly at the site without a buffer strip. However, throughout the study (1974-1980) the trophic compositions of the benthic communities of all three sites and seasons were numerically dominated by collectors, followed by collector-scrapers and collector-predators. Shredders and scrapers never comprised a major proportion of the benthic fauna (Tables 9-11).

4.3.6 Pre- and Post-Logging Periphyton Biomass at Sites 630m and 1480m

No significant yearly differences were found for periphyton biomass (mg/cm^2) estimates between sites or seasons (one-way ANOVA). The same result was obtained when periphyton biomass estimates were categorized into pre- and post-logging values (Table 12), and the means compared with a t-test. Although not significant, periphyton biomass at sites 630m and 1480m were higher after logging in the transitional and winter periods (Table 12).

4.3.7 Leaf Litter Input at the 1980 Sampling Sites

In the second year after logging, coniferous leaf litter input at site 1480m (no buffer zone) was negligible, but at site 630m (with a buffer zone), except for lower accumulations from February to May, a uniform input occurred throughout the rest of the year (Figure 7a and 7b). However, at the unlogged site (TRC), coniferous litter input was highest in the early fall (September, October) and spring (April), total litter accumulations were significantly higher than at site 630m, and annual coniferous input was more than twice the amount at site 630m (Table 13).

The seasonal patterns of deciduous litter accumulation along the streambank of the logged sites with or without buffer zones were similar and, accumulations during their periods of maximum input (August-November) were significantly higher than at the unlogged site (Figures 8a-8c). The input at all three sites was similar from November through July. Although the deciduous input at the unlogged site was irregular during the year and amounted to less than 50% of that at sites 1480m and 630m, the sum of coniferous and deciduous leaf litter at site TRC was 24% greater than site 1480m, and only 18% less than at site 630m (Table 13).

Table 12. Mean chlorophyll a values (mg/cm^3) at 630m and 1480m during the pre- (1974-1976) and post-logging (1977-1979) summer, transitional and winter periods.

	630 m		1480 m	
	Pre	Post	Pre	Post
Summer	2.18	1.17	2.45	1.64
Transitional	1.64	1.78	1.68	2.33
Winter	.74	1.88	.45	2.97

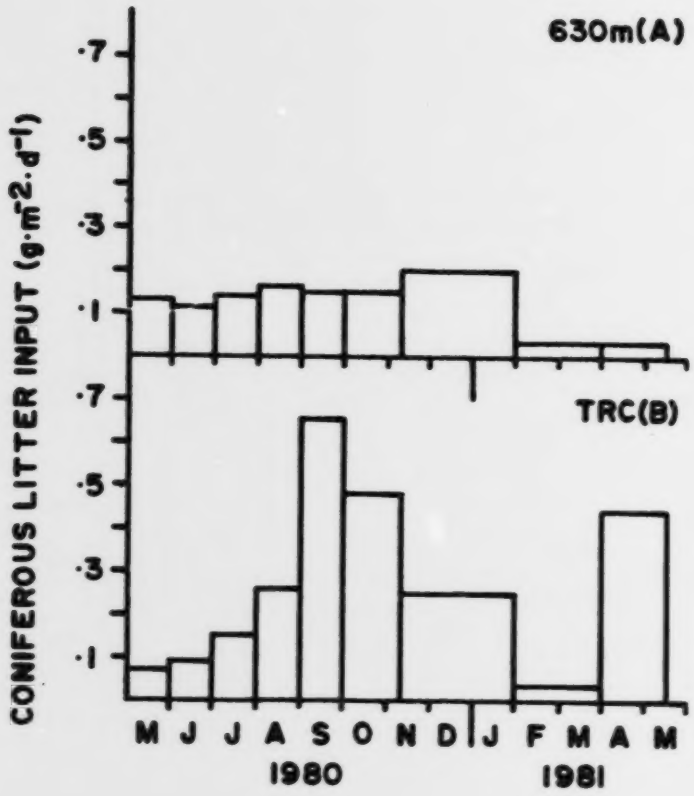

Figure 7. Coniferous litter input ($g \cdot m^{2} \cdot d^{-1}$) at sites 630m and TRC over the period 1 May 1980 to 13 May 1981. Input to site 1480m was negligible.

TABLE 13. The coniferous, deciduous and total litter input (g/m^2) at 630m, 1480m and TRC over the period 1 May 1980 to 13 May 1981.

	Deciduous	Coniferous	Total
630m	148	44	192
1480m	116	0	116
TRC	54	103	157

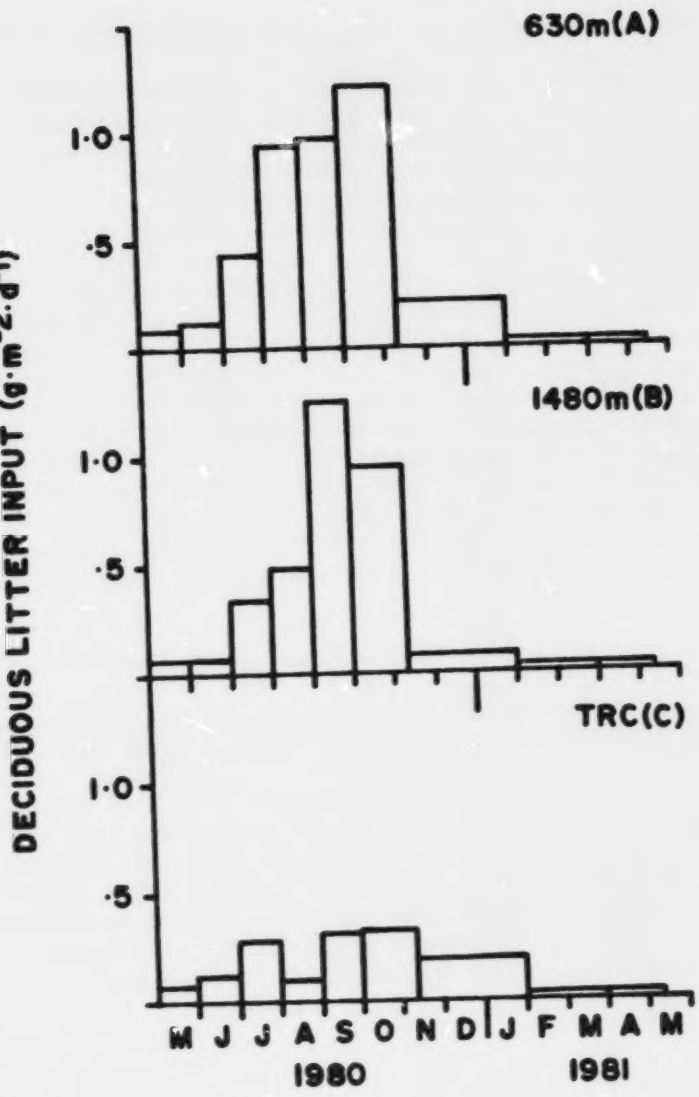

Figure 8. Deciduous litter input ($g \cdot m^{-2} \cdot d^{-1}$) at sites 630m, 1480m and TRC over the period 1 May 1980 to 13 May 1981.

4.3.8 Benthic Detritus at the 1980 Sampling Sites

The unlogged site (TRC) had significantly more coarse detritus than either of the logged sites during each sampling period (Figure 9a-c). The standing crop of coarse detritus at site TRC was highest in November immediately following maximum litter input, and was substantially reduced by January after several winter spates had occurred (Figure 9c). The seasonal trends at sites 630m and 1480m were irregular, although standing crop of coarse detritus at site 630m was higher than at site 1480m in June, August and January (Figures 9a and 9b).

Fine detritus in the substrate of the unlogged site was always significantly higher than at sites 1480m and 630m, except in January when no significant differences between sites were recorded, and June when the estimates for sites TRC and 630m were similar (Figures 9a-c). Amounts of fine detritus at the unlogged site paralleled those of the coarse detritus and reached a maximum in November (Figure 9c). Fine detritus standing crop at site 630m was high during the summer (June, August) and exceeded the amounts at site 1480m throughout the year (Figure 9a and 9b).

4.3.9 Abiotic Measurements at the 1980 Sampling Sites

Current velocity of the three sampling sites was similar in 1980 and differences between the sites were always = 14 cm/s (Appendix II). The seasonal range in current velocity was similar at all sites with the values ranging from 16 to 40 cm/s.

The substrate composition at the sampling sites was similar throughout 1980-1981 except in June when site 1480 had a slightly greater proportion in the phi -4 to -5 range (16-64 mm), and a lower proportion between phi -1 to -3 (2-8 mm) (Figures 10a and 10b; 11a and 11b). However, during each sampling month the mean substrate particle size for all the sites was similar and was between phi -3 to -4.

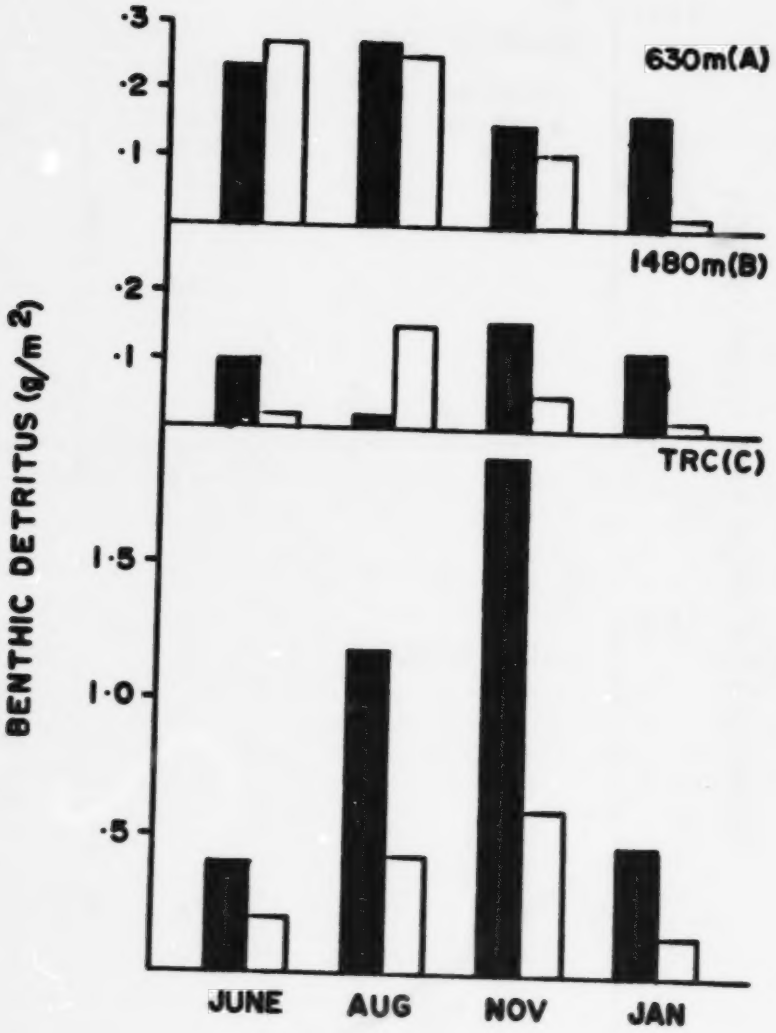

Figure 9. Mean dry mass (g/m^2) of the coarse (black bars) and fine (white bars) detritus at sites (a) 630m, (b) 1480m and (c) TRC in June, August and November 1980, and January 1981.

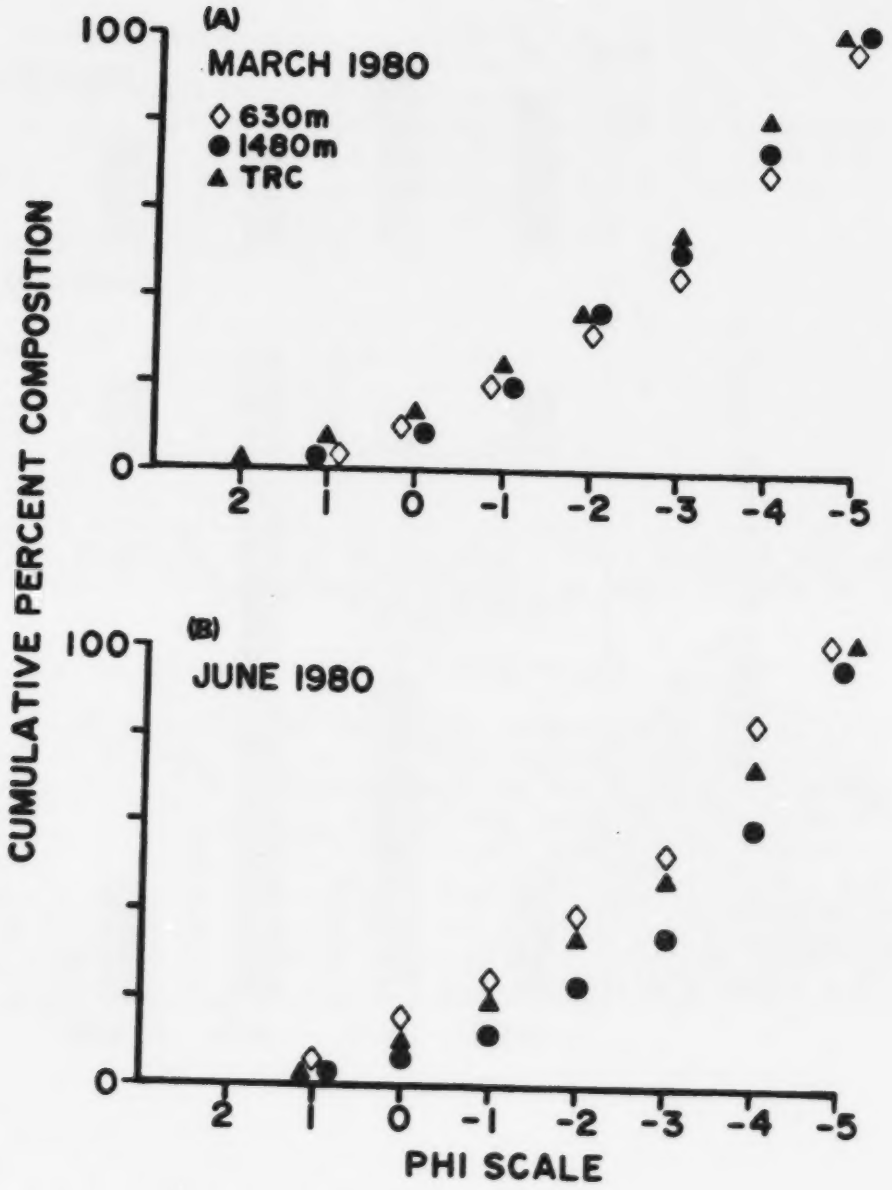

Figure 10. Cumulative substrate composition at sites 630m, 1480m and TRC in (a) March and (b) June 1980.

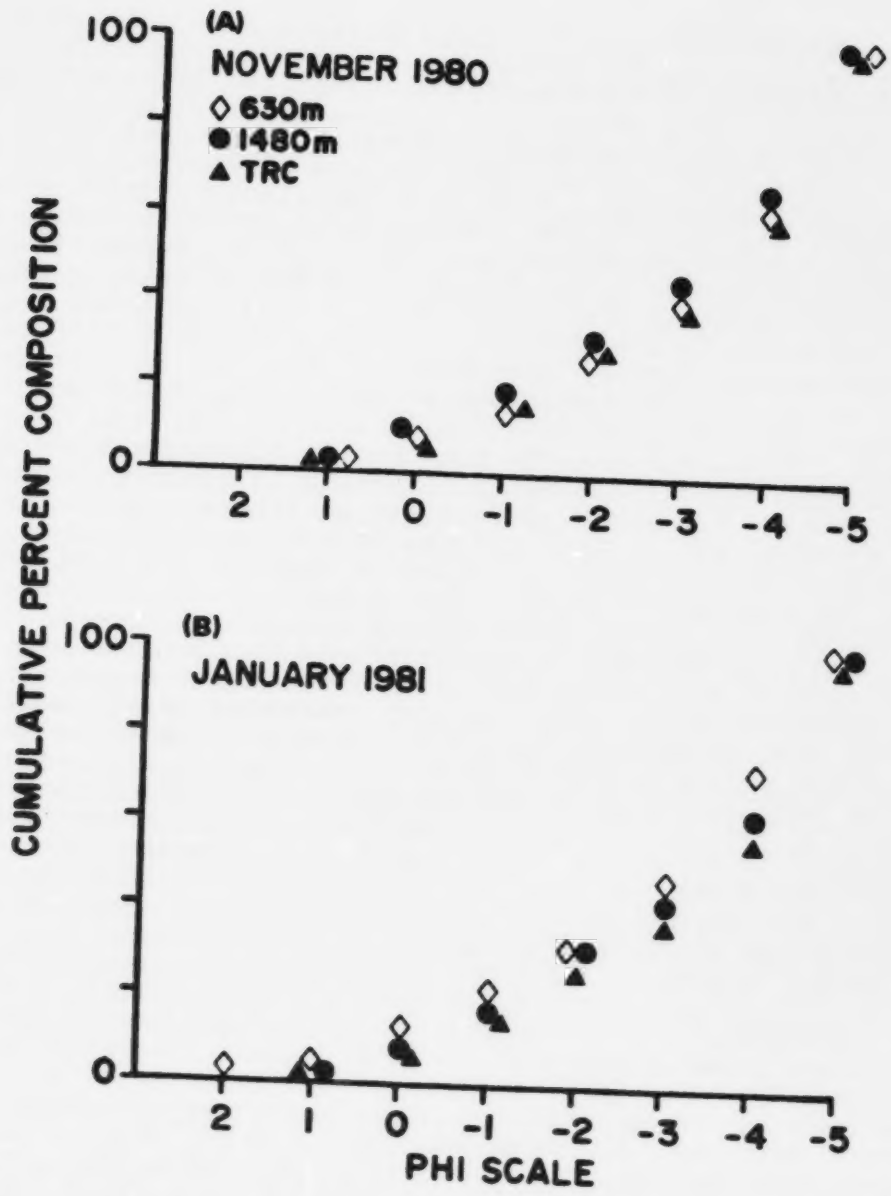

Figure 11. Cumulative substrate composition at sites 630m, 1480m and TRC in (a) November 1980 and (b) January 1981.

4.4 Discussion

4.4.1 Seasonal and Post-Logging Changes in Substrate Composition

In many of the coastal streams in Oregon and Alaska, the upper 10-15 cm of riffle substrate undergoes a winter reduction of sediment particles < 9 mm as a result of frequent storm discharge events, and the proportion of these sediments subsequently increases during the period of low summer discharge (Adams and Beschta 1980; Sheridan and McNeil 1968). Some riffles in Carnation Creek also exibited this seasonal trend during the pre- and post-logging periods, but in many other riffles, a constant proportion of this sediment size was present throughout the year (Scrivener and Brownlee 1980); Figures 10 and 11). Seasonal constancy in composition does not necessarily indicate a higher degree of stability for these riffles, as might be concluded, because estimates of substrate composition measure net, rather than gross, changes in substrate composition (Adams and Beschta 1980). Thus, if the sediments lost during the high discharge are replaced by sediments transported from upstream when the streambed restabilizes, substrate composition will be unchanged even though considerable scouring occurred.

Logging resulted in a significant 5% increase in < 9 mm sediments at both sites 630m and 1480m at all seasons (Scrivener and Brownlee 1980). Post-logging increases in sediments < 9 mm likely originated from streambank material, as these increases coincided with rapid streambank erosion along reaches with no buffer zone (site 1480m) during the high discharge period of 1978-1979 (Schultz International Ltd. 1981). Downstream transport of eroded streambank material increased the proportion of sediments even at site 630m, which had a buffer zone with stable streambanks and contained debris dams. The higher rate of bank erosion at site 1480m appeared to be a result of the removal of debris dams which formerly had provided an important structural armour for the streambank (Toews and Moore 1982).

Sediments < 0.297 mm are prevented from accumulating in Carnation Creek because of the high winter discharge, and approximately every three years a storm discharge of sufficient magnitude to remove sediment particles between 0.297-2.38 mm occurs (Scrivener and Brownlee 1980). Thus, much of the accumulated sediment load that originated from the erosion of streambanks will be removed from the stream in approximately three years.

Observed trends from other coastal streams show that post-logging increases in the rates of erosion and sedimentation eventually decline to the pre-logging levels (Beschta 1978). In Carnation Creek, this decline will likely take place within 3-5 years after logging since re-vegetation of streambanks left without a buffer zone will occur in this period. However, even with streambank re-vegetation, scouring of the streambed will continue to occur more frequently than before logging because the post-logging streambed has been more or less channelized in stream reaches without debris dams (Toews and Moore 1982).

When parts of the Carnation Creek Watershed was logged, the only significant logging-induced sedimentation occurred as a result of the rapid erosion of streambanks in reaches with all the debris dams removed and where no buffer zones were left. However, logging did not destabilize the streambank in the reach with a buffer zone and natural debris dams. Post-logging sedimentation increases in coastal streams like Carnation Creek can be prevented by leaving natural debris dams and a buffer zone only 10 m wide, as long as roads are not constructed near the stream and catastrophic mass-wasting (e.g. a landslide) does not occur.

4.4.2 Pre- and Post-Logging Periphyton Biomass

Biomass estimates of the periphyton communities of Carnation Creek (dominated by filamentous algae and diatoms (Table 12)) are among the lowest values recorded in the literature for lotic systems (Stockner and Shortreed 1976). These low pre-logging algal biomasses in Carnation Creek have been experimentally demonstrated to be largely a result of dissolved phosphorus limitations, rather than light limitations on photosynthesis. Although a rapid release of phosphorus from the terrestrial ecosystem is generally expected after clearcutting (Fredriksen 1971; Gibbons and Salo 1973), post-logging phosphorus concentrations in Carnation Creek remained surprisingly similar to the pre-logging levels, except during a few freshets immediately after slashburning in the fall of 1978. When this occurred, the nutrients were rapidly exported (Scrivener unpublished data), and were largely unavailable to the algae. If nutrients increased in Carnation Creek after logging at other times of the year, these increases were minimal and below detection limits. Therefore, even though clearcutting opened the forest canopy and greatly increased the light available for photosynthesis, a significant change in algal biomass was not observed because phosphorus apparently was still the limiting factor.

4.4.3 Impact of Logging on Leaf Litter Input

One objective of maintaining buffer zones after clearcutting is to provide the stream with an allochthonous input of a similar quantity and composition as that which occurred prior to logging. Even when maintaining buffer zones (site 630m) in Carnation Creek, clearcutting resulted in a thinning of the trees surrounding the creek because of blow down (Schultz International Ltd. 1981) and the selective logging of conifers. The result was that while the timing of the maximal deciduous input during September to November remained unchanged from the pre-logging pattern observed by Neaves (1978), annual conifer input from the site 630m buffer strip was reduced from 169 g/m^2 (Appendix 1, Neaves 1978) to 44 g/m^2 (Table 13), and annual deciduous input from 425 g/m^2 (Appendix 1, Neaves 1978) to 148 g/m^2 (Table 13).

Post-logging litter accumulation at site 630m was therefore reduced by > 60%, and the amount and pattern of deciduous input from the buffer zone was not significantly different from site 1480m, clearcut to the streambank (Figure 8). If buffer zones are to maintain normal levels of allochthonous input observed for coastal streams, the width of this buffer strip must be considerably wider than the 10 m zone left along Carnation Creek and selective logging within this zone prohibited.

The predominance of coniferous needles (68%) in the allochthonous litter accumulations at the unlogged site (TRC) (Table 13) indicates a greater importance of coniferous vegetation at this site, as compared to the pre-logging allochthonous input at site 630m, where 70% of the leaf litter was deciduous (Appendix 1, Neaves 1978). Because the allochthonous input at the unlogged site was dominated by coniferous litter, and the annual litter input total was < 30% of the pre-logging input at site 630m, the unlogged site was not indicative of the normal allochthonous input in the lower 2 km of Carnation Creek and could not be used as a post-logging control for the logged sites 630m and 1480m.

4.4.4 Impact of Logging on Benthic Detritus

Site TRC could not be used as an unlogged control for benthic detritus because it had a significantly different pre-logging allochthonous input regime compared to sites 630m and 1480m. However, post-logging comparisons could be made between sites 630m and 1480m which had similar pre-logging allochthonous inputs, and similar post-logging substrate compositions so that the potential for trapping detritus of different sizes was similar.

Although the pre-logging allochthonous inputs, and likely the standing crop of detritus, of sites 1480m and 630m were similar, after logging benthic detritus was highest in the reach with a buffer zone. The post-logging allochthonous input regimes of sites 630m and 1480m primarily differed in the absence of coniferous litter at site 1480m without a buffer zone. The between site differences in detritus appear to be partly a function of the accumulation of coniferous detritus at site 630m due to the slower decomposition of coniferous compared to deciduous litter (Anderson and Sedell 1979), and the greater scouring in the channelized reach of site 1480m which decreased the accumulation of benthic detritus.

4.4.5 Seasonal Patterns of Macroinvertebrate Composition

Discharge was a major factor influencing the macroinvertebrate faunal composition both before and after logging. In the winter, mean monthly discharge was consistently > 1 m^3/s (Figure 2), and often caused sediments < 9 mm to be flushed from many localized sections of the streambed (Scrivener and Brownlee

1980). Because of the high discharge and the downstream movement of suspended or saltating sediments that scoured the substrate, the total densities of most taxa were greatly reduced in the winter (Tables 4-6). Additionally, the high winter discharge had an indirect effect on densities by reducing the amounts of the macroinvertebrate food resources, periphyton (Table 13) and benthic detritus (Figure 9).

Although the high winter discharge reduced densities of all taxa to their lowest values of each year, this naturally occurring perturbation changed the species composition, and thus was not a non-selective stress which detrimentally affected all taxa according to their proportions in the substrate. Two diagnostic taxa (Alloperla and B. tricaudatus) actually increased in proportional abundance in the winter because scouring decreased their densities less than other taxa. Clearly, Alloperla and B. tricaudatus must be able to avoid some of the detrimental effects of scouring, perhaps by moving to more stable substrate microhabitats during high discharge.

Throughout much of the transitional period and all of the summer period, the riffle substrate was more stable than in the winter because the lower discharge from April to October seldom scoured the substrate, and sediments < 9 mm accumulated in the substrate (Scrivener and Brownlee 1980). During this period of higher substrate stability, the densities of most of the diagnostic taxa increased apparently because (1) the standing crop of the macroinvertebrate food resources, periphyton and benthic detritus increased, and (2) because April to October is the period of recruitment of new cohorts for most species of Chironomidae, Ephemeroptera, Plecoptera and Trichoptera. The benthic macroinvertebrate species in Carnation Creek have adapted their life histories to utilize the annually recurring period of maximum food abundance and substrate habitat stability as the time of maximum growth and reproduction.

4.4.6 Seasonal Composition of Macroinvertebrate Trophic Guilds

Trophic guild composition was unexpectedly similar throughout the year, before and after logging (Tables 9-11), despite the seasonal changes in food resources and the seasonally distinct faunal composition of the benthic communities. However, densities of all functional feeding groups were significantly decreased in the winter, relative to transitional and summer period densities, because of frequent scouring of the substrate during storm discharges. This indicates that, as was established for the ten diagnostic taxa, the abiotic variables of scouring and discharge were primary factors affecting the seasonal abundances of functional feeding groups, while seasonal differences in food resources appeared to be of secondary importance.

From the generalizations of the River Continuum Concept (RCC) (Vannote, Minshall, Cummins, Sedell and Cushing 1980), it was anticipated that shredders would be numerically important in

the fall when CPOM litter input was highest, and scrapers and collector-scrapers would dominate during the summer period of higher autochthonous production. In contrast, throughout the pre- and post-logging periods, scrapers and CPOM shredders were never numerically important trophic guilds in Carnation Creek, regardless of the sampling site or season considered. Instead, the pre- and post-logging macroinvertebrate communities were composed largely of collectors, collector-scrapers and collector-predators, all of which utilize FPOM food sources. Therefore, contrary to the RCC predictions, formation of FPOM must proceed mostly by physical abrasion and microbial decomposition of CPOM, since few shredders are present to comminute CPOM.

4.4.7 Impact of Logging on Macroinvertebrate Communities

After the forest was clearcut to the streambank at site 1480m, the densities of most macroinvertebrate taxa were reduced from their comparable pre-logging estimates for one or more seasonal period. Although the winter had always been an annually recurring period of streambed perturbation, at site 1480m after logging, winter scouring caused greater density decreases because of the increased input of < 9 mm sediments from the eroded streambanks. Significantly lower post-logging macroinvertebrate densities were also recorded at site 1480m in the summer and transitional periods with low discharge (Tables 4 and 5), when scouring could not be the cause of these reductions. As sediments < 9 mm are deposited and intrude into the streambed during low discharge (Scriviner an Brownlee 1980), the effect of the increased sediments during the summer and transitional periods was to fill interstitial spaces, which reduced the permeability of substrates to intra-substrate water flow, and decreased dissolved oxygen levels in the post-logging streambed (Scrivener and Brownlee 1980). The lower amounts of intra-substrate dissolved oxygen and water flow, combined with the filling of interstitial spaces, reduced the available substrate habitat for macroinvertebrates, and at least partially explains the post-logging decreases of macroinvertebrate density in the summer and transitional periods. However, the decreased post-logging allochthonous energy input at site 1480m must also have lowered macroinvertebrate densities during these two seasons.

Post-logging densities of macroinvertebrates at site 630m also decreased after logging, but the < 10 m wide riparian buffer zone ameliorated some of the detrimental effects of logging. During the post-logging winters, the downstream transport of sediments eroded from the streambanks of the site 1480m reach caused decreases in macroinvertebrate density for at least three winters (1978-1980) (Appendix IX). Since the total density of the diagnostic macroinvertebrate taxa at site 630m decreased by only 24% from the pre-logging winters, whereas the comparable decrease at site 1480m was 41%, the effects of scouring of the

substrate were less severe at site 630m. Total density in the winter at site 630m was thus higher than at site 1480m after logging (Table 6).

In the summer and transitional periods before logging, the total density of the diagnostic taxa at site 630m was lower than the comparable site 1480m densities. However, after logging, this trend was reversed with total densities at site 1480m decreased by 50% (Tables 4 and 5). Since post-logging sediment increases were similar at sites 630m and 1480m, the greater density decrease observed at site 1480m in the summer and transitional periods can not be due to direct sedimentation effects. The major environmental difference between these sites was the significantly higher allochthonous input from the streambank of site 630m, with higher post-logging benthic detritus standing crop. The greater post-logging decreases in total density at site 1480m, as compared to site 630m, appear to result from the low post-logging standing crop of detritus.

The effects of logging at site 630m were thus less severe because the buffer zone provided important energy subsidies to the macroinvertebrate communities during the summer and transitional periods. However, as the allochthonous input from the < 10 m buffer zone was greatly decreased compared to pre-logging estimates, it seems likely that the post-logging macroinvertebrate density decreases at site 630m are the result of this lower post-logging allochthonous input, and the detrimental effects of sedimentation.

The Carnation Creek results indicate that logging of a small coastal stream without leaving a buffer zone or debris dams, significantly increases the rates of streambank erosion and < 9 mm sediment input. The detrimental effect of these sediment increases on macroinvertebrate communities varied seasonally between scouring of the substrate in the winter, and intrusion into the substrate in the summer and transitional periods. Logging of the streambank also decreased macroinvertebrate densities because allochthonous input to the stream was significantly reduced.

Macroinvertebrate communities were less detrimentally affected by logging when a < 10 m wide riparian buffer zone and natural debris dams were left along the stream. Logging with a buffer zone reduced the effect of logging-related scouring on macroinvertebrates in the winter, and added a greater amount of allochthonous input to the stream in the summer and transitional periods than when the streambank was clearcut, and thus indirectly provided food for macroinvertebrate detritivores.

The Carnation Creek investigation establishes that, unlike the findings reported for California (Newbold, Erman and Roby 1980) or Oregon (Murphy and Hall 1981) coastal streams, macroinvertebrate densities do not necessarily increase when logging opens the canopy. In these other coastal streams, the macroinvertebrate food base appeared to shift from allochthonous detritus to algal biomass because autochthonous primary production greatly increased after logging, and leaf litter input was reduced. However, since primary production did not increase

after logging at Carnation Creek, the amounts of energy available to the post-logging macroinvertebrate communities were greatly reduced, particularly in the reach without a buffer zone. This reduction in available energy in Carnation Creek underscores the importance of leaving a buffer zone along the streambank so allochthonous energy subsidies remain similar to pre-logging levels. Furthermore, a buffer zone stabilizes the streambank and prevents sedimentation.

Clearly, the streambank of coastal streams is a major interface through which energy is transferred from the terrestrial ecosystem and by which sedimentation inputs are mediated. Logging activities along this interface cause environmental changes to the stream ecosystem that can be detrimental to macroinvertebrates during all seasons. If coastal streams are to be maintained as productive rearing habitats for salmonid fry, guidelines for the management of streams must attempt to protect this streambank interface. From the Carnation Creek findings, it would appear that the maintenance of buffer zones and debris dams should be focal points for these guidelines.

5. EXPERIMENTAL MANIPULATION OF DETRITUS AND SUBSTRATE COMPOSITION

5.1 Introduction

Particulate detritus (sensu Boling, Goodman, Van Sickle, Zimmer, Cummins, Peterson and Reice 1975) derived from terrestrial leaf litter can comprise a major portion of the total energy budgets of streams draining temperate forests and it is an important food resource of macroinvertebrates (Minshall 1967; Fisher and Likens 1973; Anderson and Sedell 1979; Vannote, Minshall, Cummins, Sedell and Cushing 1980). Utilization of detritus by macroinvertebrates varies with its microbial conditioning (relative degree of microbial colonization) and quality (Cummins 1974), with high-quality detritus (e.g. alder) processed more rapidly than low-quality detritus (e.g. hemlock) (Anderson and Sedell 1979). Additionally, a decrease in particle size will provide a greater surface area for microbial colonization, and tend to increase the rate of microbial conditioning of detritus resulting in a higher quality detritus (Peterson and Cummins 1974; Boling, Goodman, Van Sickle, Zimmer, Cummins, Peterson and Reice 1975), and increased detritivore growth rates (Ward and Cummins 1979).

Thus, detritus quality, quantity and particle size have the potential to directly affect the distribution and abundance of macroinvertebrate detritivores. However, with the exception of Egglishaw's (1964) pioneering experiments, field manipulations have been restricted to the comparison of substratum with or without detritus (Rabeni and Minshall 1977; Peckarsky 1980), and only large particulate detritus (5 to 10 mm leaf strips) has been quantified (Peckarsky 1980).

Macroinvertebrate distribution and abundance has also been correlated with substrate composition (Linduska 1942; de March 1976), and several researchers have attempted to determine the importance of substrate by examining colonization of different substrate treatments under conditions of similar current velocity (Allen 1975; Minshall and Minshall 1977; Williams and Mundie 1978; Khalaf and Tachet 1980; Reice 1980; and Williams 1980). However, since detritus accumulation in these studies was either not measured, or measured but not experimentally controlled, the influence of detritus on their results can not be determined. Thus, because of poor experimental control, generalizations concerning the relative importance of detritus and substrate as microdistribution factors are impossible to formulate.

Since logging can affect substrate and detritus composition, field manipulative experiments were designed to test the following hypotheses:

1) Does substrate size and heterogeneity influence macroinvertebrate distribution and abundance if detritus quality and quantity are controlled?

2) Can changes in detritus quality and quantity within a standardized substrate composition affect macroinvertebrate distribution and abundance?

By manipulating these interrelated variables in separate experiments, a more accurate prediction of the effects of logging-related changes in substrate composition and detritus standing crop likely can be achieved.

5.2 Study Area

The experimental riffle (1.6 x 2.3 m) was located 10 m above the main discharge gauging station (B weir) and 0.6 km above the estuary (Figure 1). Riparian vegetation was primarily composed of red alder, salmonberry, and salal. Large western hemlock, Sitka spruce or western red cedar were also sometimes present.

5.3 Methods

5.3.1 Variable Substrate With Fixed Detritus

Substrate was obtained from dry areas of the streambed and sieved into classes corresponding to the modified Wentworth scale (Cummins 1962). Five substrate mixtures were produced: I-S, homogeneous large gravel (9.5 - 16.0 mm); II-S, homogeneous small pebbles 16.0 - 31.5 mm); III-S, a 1:1 volumetric mixture of gravel and pebbles; IV-S, a 1:1 gravel and pebble mixture with the interstices filled with small-medium gravel and coarse sand (1.0 - 9.5 mm); V-S, an identical mixture to treatment IV-S with cobble (50.0 - 80.0 mm) on the surface and which approached the habitat complexity of the natural substrate. Detritus of fixed quality and quantity was added to each of these five substrate types, while in a sixth treatment (VI-S) with the same substrate composition as treatment III-S, no detritus was added. The range in substrate composition between treatments I-S to V-S was chosen because it encompasses the majority of compositions used in previous experiments (e.g. Minshall and Minshall 1977; Rabeni and Minshall 1977; Williams and Mundie 1978; Khalaf and Tachet 1980; Reice 1980; Williams 1980). Similarly, the quantity of detritus corresponds to the amounts used by Rabeni and Minshall (1977) and Peckarsky (1980).

The quality and quantity of detritus in treatments I-S to V-S were standardized to reduce the potential effects of the detritus-substrate interaction upon macroinvertebrate colonization. Detritus was produced by collecting alder leaves from trees which had been felled five weeks earlier, followed by incubation of the leaves in the dark for four weeks in flowing creek water that was filtered to remove any invertebrates. Immediately prior to experiment initiation, the conditioned leaves were mechanically shredded in a blender and wet sieved into fine (230 - 850 µm) and medium (850 µm - 2.0 mm) fractions.

Four cylindrical plastic containers (.015 m^2, 6.5 cm deep), with two 230 µm mesh windows (21.0 x 3.5 cm) to allow water flow through the container, were filled with each of the substrate treatment types, and 7.5 g wet mass (1.5 g dry mass) of alder detritus added (fine to medium ratio 2:1). Surface rocks of the same size as those in each container, and with visually similar periphyton growth, were taken from an upstream riffle and used as the top layer of each container. The containers were momentarily sealed while being implanted into the experimental riffle with the upper edges flush with the streambed surface. The covers were immediately removed, and the containers left in the stream for a 31 day colonization period (21 July - 21 August 1980).

Since the abiotic loss of alder detritus from the containers could change the experimental treatments, this loss was measured by soaking substrate mixtures identical to III-S in concentrated formalin, and placing them immediately downstream of the experimental riffle (III-SF). These containers were removed every 5-7 days during the experiment, immersed in formalin for 4 hours, and replaced in the stream. Contents of the containers were preserved at the end of the experiment and the dry mass of the detritus determined.

The amount of fine sediment accumulated in each substrate type was estimated by placing four replicate sediment traps (.005 m^2) (Welton and Ladle 1979) per treatment into the experimental riffle. Surface current velocity 2.5 cm above the substrate was measured for each substrate treatment with a Gurley pygmy current meter, while the salt dissolution technique of Rabeni and Minshall (1977) was used to measure intra-substrate current velocity in containers placed immediately downstream of the experimental area. Discharge was continuously monitored by Environment Canada.

The interstitial space of each substrate treatment type was measured in the laboratory by adding water to containers with the five substrate mixtures, and recording the decanted water volume. Surface area of particles in I-S, II-S and III-S was determined by inking the surface of a known volume of rocks with a 1 cm^2 stamp.

The containers were carefully removed upon completion of the colonization period, and community respiration was measured on the undisturbed sediments before the macroinvertebrates and detritus from each container were preserved in 10% formalin. Animals were sorted under 12x magnification, identified to the lowest taxonomic level possible, enumerated, and the dry biomass of each taxon measured using a Cahn 25 Automatic Electrobalance. Dry mass of the organic and inorganic material was also determined as described in Section 4.2.

5.3.2 Variable Detritus With Fixed Substrate

With a fixed 1:1 substrate composition of gravel (9.5 - 16.0 mm) and pebbles (16.0 - 31.5 mm), four detritus treatments (each with five replicates) were established: I-D, no detritus;

II-D, hemlock detritus (99 g/m^2); III-D, low alder detritus (67 g/m^2); and IV-D, high alder detritus (133 g/m^2). The detritus for these treatments was produced from alder leaves and brown hemlock needles using the methods described in section 5.3.1. Detritus quantities cover the range used in previous detritus manipulation experiments (e.g. Egglishaw 1964; Minshall and Minshall 1977; Rabeni and Minshall 1977; Peckarsky 1980).

Each detritus treatment was produced by placing the appropriate detritus (fine to medium ratio fixed at 2:1) along with the standardized substrate in cylindrical containers (.008 m^2, 6.5 cm deep) with two 230 µm mesh windows (10 x 3 cm). The containers were momentarily covered while being embedded flush with the streambed surface. After 4 weeks (29 July - 26 August 1980) the containers were removed and community respiration measured before the invertebrates and detritus were sorted and preserved (Section 5.3.1). All macroinvertebrate samples were sub-sampled (Wrona, Culp and Davies 1982) before enumeration and biomass determination (Section 5.3.1). The detritus from each container was wet seived and the ash-free dry mass determined for the 106 - 233 µm, 233 - 850 µm, 850 µm - 2 mm, and > 2 mm size fractions. The accumulated organic and inorganic sediments in the control treatment (I-D) was used to indicate whether or not natural sedimentation had altered the detritus treatments (II-D to IV-D).

5.3.3 Laboratory Community Respiration Technique

The respiration chamber (Figure 12a) consisted of a bottom container made of PVC piping, a plexiglass plate used for covering the bottom section in the field, and a plexiglass top section containing a brass paddle wheel turned by a variable speed drill via a pulley system (Figure 12b). In the field each substrate container was inserted into the watertight bottom section and sealed to minimize disturbance during transport (0.5 km for 20 min) to the laboratory. In the laboratory each chamber was placed in a water bath at ambient creek temperature, the cover removed, and the top section of the respirometer fitted over the bottom ensuring that no air bubbles were inside the chambers. A pH probe was inserted through a gasket seal in the top section, and pressure differences were equalized by inserting a syringe needle (18 gauge) through a Vacutainer septum seal. The water bath was covered with black plastic, the paddle wheel was started (100 rpm) to prevent vertical stratification, and a 1 h acclimation period begun to allow primary production to cease (Hargrave 1969). After this period, pH was recorded every 10 min for 1 h using a Fisher Accumet Model 620 meter equipped with a five probe capacity, Model 157 switchbox and glass electrodes. Changes in pH were converted to the release of CO_2 mg/l using the equations of Vollenweider (1969).

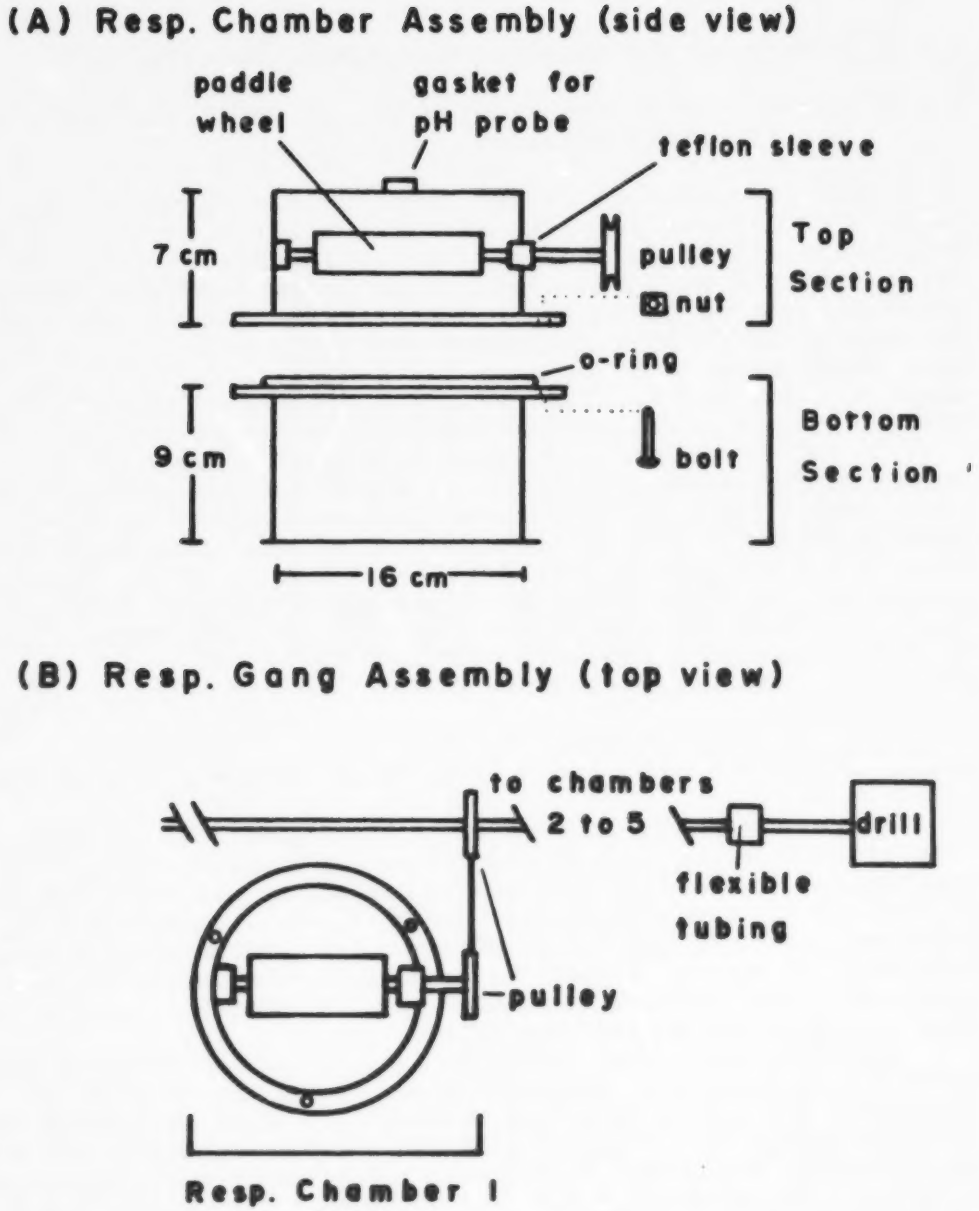

Figure 12. (a) Side view of the top and bottom sections of the community respirometer; and (b) top view of the respirometer gang assembly.

5.4 Substrate and Detritus Experiment Results

5.4.1 Effects of Abiotic Environmental Conditions on Experimental Variables

Water temperature ranged from 12-14.5 ^{o}C during the experiment. Current velocity also was similar throughout the experiment (15-31 cm/sec) and no significant differences between the treatments were recorded. Mean daily discharge ranged from .042-.062 m^3/sec for most of the experimental period, however, during the first week discharge reached a peak of .116 m^3/sec. Only small amounts of organic sediments (i.e. detritus) were suspended and re-deposited by these discharge levels, since at the end of the experiment accumulations of detritus accounted for < 60 mg of the detritus in each treatment container. Furthermore, the amount of detritus deposited was similar for all treatments. By subtracting the deposited detritus from the total amounts of detritus found at the end of the experiment in the substrate (I-S to V-S) and detritus (II-D to IV-D) treatments, losses of the experimentally fixed quantities of detritus were estimated to be 14 to 17%. Inorganic sedimentation, as measured by sediment traps, was only 200 mg (<.001%) of the total substrate mass per container.

5.4.2 Substrate Experiment Results (Treatments I-S to VI-S)

Intra-substrate current velocity, substrate surface area and interstitial space varied significantly between substrate treatments (Table 14). Interstitial space was negatively related to surface area being highest in II-S, and lowest in I-S. Conversely, intra-substrate current was positively related to interstitial space, except in treatment II-S where it was unexpectedly low because the salt tablets were in the dead water zone of large substrate particles.

Although the total amount of detritus was reduced in all substrate treatments, the losses attributable to abiotic processes did not affect the initial 2:1 fine to medium ratio of particle sizes in treatment III-SF. However, the final ratios of the particle sizes for treatments with macroinvertebrate colonization increased to 2:7 - 4:1 (Figure 13). Comparing all substrate treatments, the decreases in medium sized particles were significantly higher in I-S and II-S, and the loss of fine detritus was significantly greater in II-S.

Community respiration varied significantly between substrate types. Treatment IV-S with the greatest amount of fine detritus had a significantly higher respiration rate than II-S (Table 14) which retained the least fine detritus. Respiration was positively correlated with both detritus mass and macroinvertebrate biomass (r^2 = .77), but subsequent partial correlation analyses indicated the significant relationship was between community respiration and fine detritus (r^2 = .51).

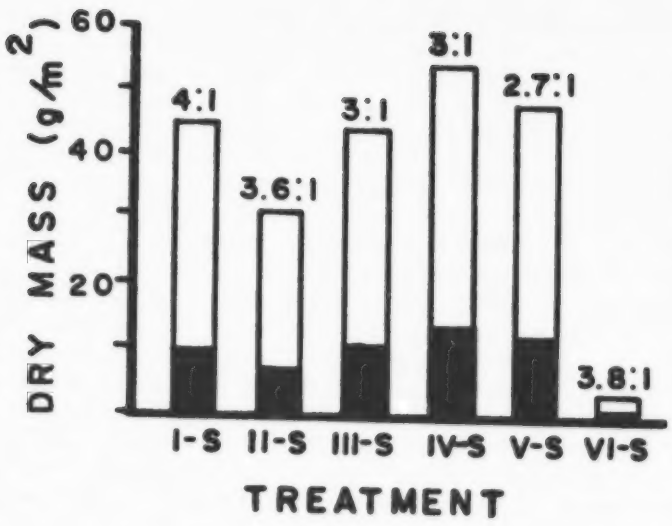

Figure 13. Mean dry mass (g/m^2) of the amount of fine (white) and medium (black) detritus, and the fine to medium ratio of treatments I-S to VI-S at the end of the experiment.

Table 14. Mean value of community respiration (CO_2 mg/l), intra-substrate current (cm/sec), surface area (m^2) and interstitial space (cm^3) (Community respiration data were not available for I-S or VI-S due to equipment failure).

Substrate Treatment	Community Respiration	Intra-Substrate Current	Surface Area	Interstitial Space
I-S	-	6.4	.31	420
II-S	.50	3.5	.11	474
III-S	.79	9.3	.21	435
IV-S	.96	4.2	>.21	<435
V-S	.84	3.3	>.21	<435
VI-S	-	9.3	21	435

A Model I ANOVA demonstrated that the mean density and biomass of only 3 of 19 macroinvertebrate taxa which colonized the containers showed significant differences between the treatments with detritus added (I-S to V-S) (Figure 14). The trends of low density and biomass of Thienemannimyia in II-S were associated with depressed levels of detritus, but trends for B. tricaudatus and Ameletus showed no correlations with substrate particle size, interstitial space, surface area, intra-substrate current, detritus mass or community respiration.

The mean densities and/or biomasses of four taxa were significantly correlated with the mass of fine and medium detritus in substrates I-S to V-S at the end of the experiment (Table 15). Biomass of the shredders Zapada cinctipes and Polypedilum (Polypedilum) which comminute medium particles, and the collector Micropsectra were negatively correlated with medium detritus mass, and positively correlated with fine detritus mass. Densities of Z. cinctipes and Thienemannimyia were positively correlated with fine detritus mass, but only Z. cinctipes showed a negative correlation with medium detritus mass.

Large differences in substrate particle size, and small differences in detritus retention did not significantly affect the distribution of most taxa when detritus quantity and quality were standardized. However, treatment III-S with detritus had a higher biomass and density for nine taxa compared to treatment VI-S without detritus (Table 16). These nine taxa comprised over 60% of the macroinvertebrate density and biomass of III-S, and except for two predators (Skwala and Thienemannimyia), were shredders or collectors.

5.4.3 Detritus Experiment Results (I-D to IV-D)

Ultra-fine detritus (106 - 233 µm) was not initially present, but at the end of the detritus experiment, significant differences in the amount of this size fraction present were found between treatments. The greatest amounts of ultra-fine detritus were in the alder detritus treatments (III-D and IV-D) where the fine to medium detritus ratio of the low (III-D) and high alder (IV-D) treatments increased to 3.9:1 and 3.2:1, respectively (Figure 15). However, in the hemlock detritus (II-D) and formalin treatments (III-SF) the original 2:1 ratio of fine to medium detritus was maintained. Additionally, organic sedimentation was < 40 mg per container in all the treatments, but did not change the detritus ratios.

ANOVA indicated that 12 of the 20 colonizing macroinvertebrate taxa had significantly different densities or biomasses in the four detritus treatments, and SNK tests showed that compared to no detritus or hemlock detritus, alder quantity significantly changed the density and/or biomass of these 12 taxa (Table 17). Relative to the no detritus or hemlock treatments, the low alder detritus treatment increased the density and/or biomass of nine taxa, and decreased three Chironomidae (Corynoneura, Synorthocladius, Thienemanniella) (Table 17; Figures 16 and 17). In the high alder treatment six taxa showed

significantly higher density and/or biomass as compared to the control, and six taxa significantly decreased (Table 17; Figures 16 and 17). The six taxa which were decreased by the high alder treatment included the three Chironomidae listed above, plus C. ramaleyi and Baetis hageni (Ephemeroptera), and Orthocladius (Chironomidae) (Table 17). Chironomidae density and biomass in hemlock detritus was similar to the no detritus treatment, but Ephemeroptera abundance decreased in hemlock detritus (Figures 16 and 17).

Community respiration was significantly different between treatments with the respiration in I-D (.16 mg CO_2/l) and II-D (.17 mg CO_2/l) similar and significantly lower than the values for III-D (.26 mg CO_2/l) and IV-D (.32 mg CO_2/l).

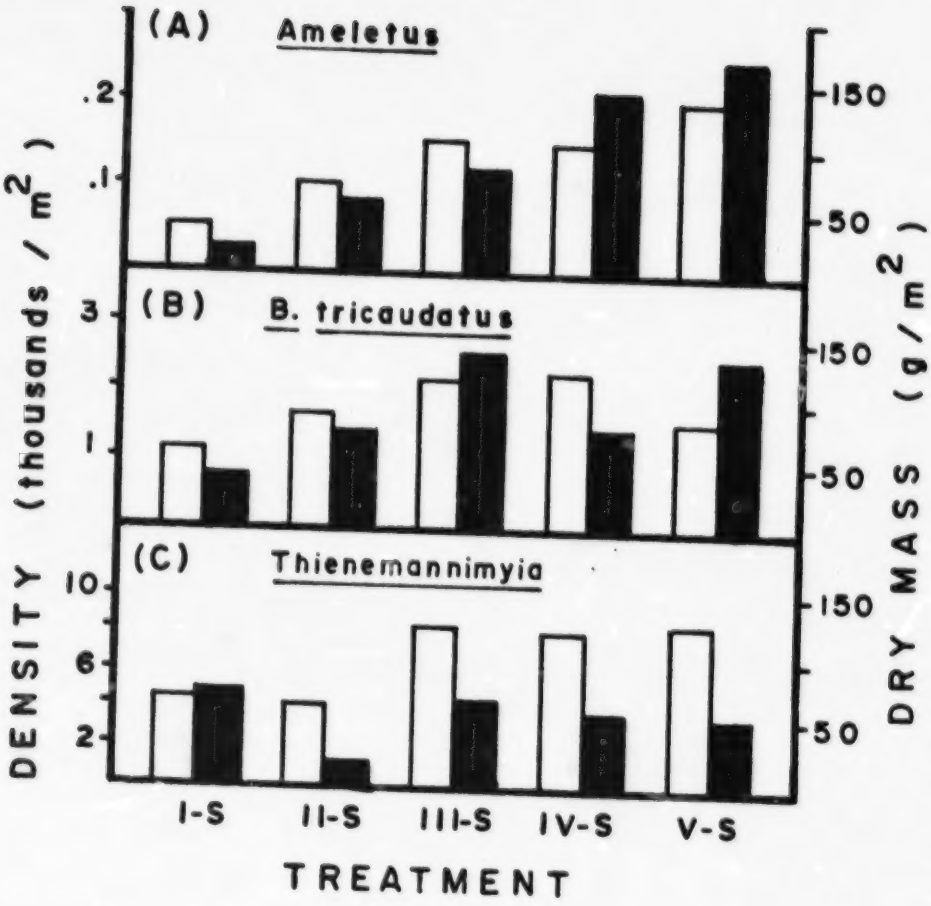

Figure 14. Mean density (thousands/m^2) (white) and biomass (g/m^2) (black) of Ameletus, B. tricaudatus and Thienemannimyia in treatments I-S to VI-S.

Table 15. Multiple r^2 values and the partial correlation coefficients for the four macroinvertebrate taxa which showed significant multiple correlation coefficients between density (no/m^2) or biomass (g/m^2) and fine and medium detritus.

	Multiple r^2		Correlation with Fine Detritus		Correlation with Medium Detritus	
Taxon	$No./m^2$	g/m^2	$No./m^2$	g/m^2	$No./m^2$	g/m^2
Micropsectra	-	.31	-	+.55	-	-.44
Polypedilum (*Polypedilum*)	-	.33	-	+.40	-	-.57
Thienemannimyia	.27	-	+.40	-	-	-
Zapada cinctipes	.26	.38	+.39	+.50	-.51	-.62

Table 16. Biomass (g/m^2) and density (thousands/m^2) for the nine macroinvertebrate taxa which exhibited significant differences between treatments III-S and VI-S, and the totals for all 19 taxa. (15 taxa with mean treatment values of <1 individual per replicate were omitted from the analysis.)

Taxa	g/m^2		thousands/m^2	
	III-S	VI-S	III-S	VI-S
Baetis tricaudatus	.13	.04	2.18	.86
Brillia	.56	0	3.70	0
Chironomidae pupae	.40	.01	1.85	.07
Micropsectra	.04	.01	3.10	1.12
Parametriocnemus	<.01	0	.20	0
Polypedilum (Polypedilum)	.69	.01	8.05	.66
Skwala	.13	.01	1.85	.06
Thienemannimyia	.07	.01	8.58	2.05
Zapada cinctipes	.01	<.01	.07	.07
Total for all 19 taxa	3.17	1.58	43.30	17.09

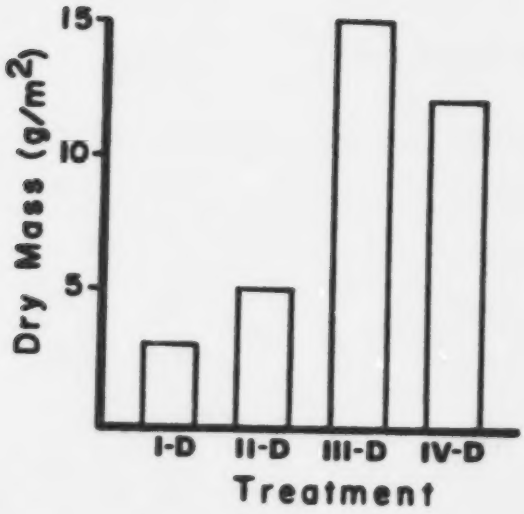

Figure 15. Mean dry mass (g/m^2) of the accumulated ultra-fine detritus (106-233μm) in I-D to IV-D and the abiotic treatment.

Table 17. Summary of the SNK test results showing that the low (III-D) and high (IV-D) alder detritus treatments either increased (+) or decreased (-) macroinvertebrate abundance relative to the no detritus (I-D) and hemlock (II-D) treatments. (n.s. indicates the ANOVA was not significant).

Taxa	Alder Detritus Effect			
	Density		Biomass	
	Low (III-D)	High (IV-D)	Low (III-D)	High (IV-D)
Ephemeroptera				
Cinygmula ramaleyi	+	-	+	-
Baetis hageni	+	-	+	-
Chironomidae				
Brillia	+	+	+	+
Chironomidae pupae	n.s.	n.s.	+	+
Corynoneura	-	-	-	-
Micropsectra	+	+	+	+
Orthocladius	+	-	+	-
Parametriocnemus	+	+	+	+
Polypedilum (Polypedilum)	+	+	+	+
Synorthocladius	-	-	n.s.	n.s.
Thienemanniella	-	-	n.s.	n.s.
Thienemannimyia group	+	+	n.s.	n.s.

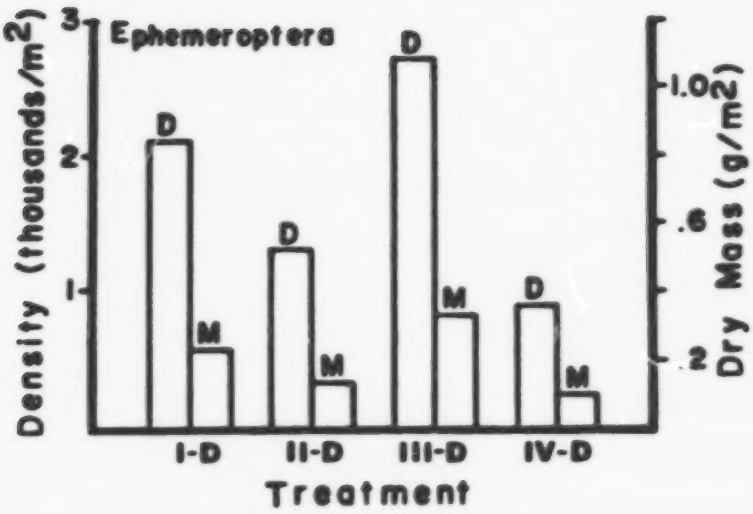

Figure 16. Mean density (thousands/m^2) and mean dry biomass (g/m^2) of the Ephemeroptera significantly affected by treatments I-D to IV-D. (D = density; M = dry biomass)

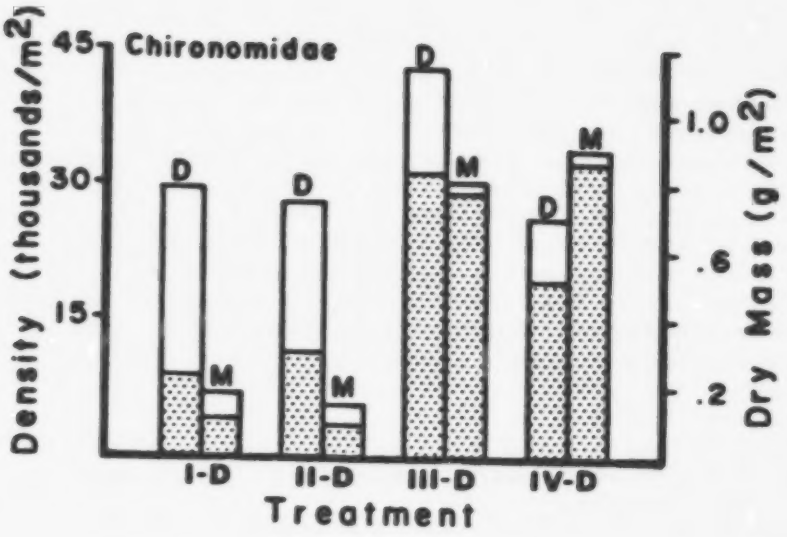

Figure 17. Mean density (thousands/m^2) and mean dry biomass (g/m^2) of the Chironomidae significantly affected by treatments I-D to IV-D. The alder detritus treatments (III-D and IV-D) either affected these taxa positively (shaded) or negatively (unshaded). (D = density; M = dry biomass)

5.5 Discussion of Substrate and Detritus Experiments

5.5.1 Constancy of Experimental Conditions

For field manipulative experiments to be valid, it must be demonstrated that environmental conditions during the experiment did not significantly alter the treatment variables, and that treatment replicates were constant. The Carnation Creek substrate and detritus experiments meet these requirements because the minute amounts of organic and inorganic sedimentation during the colonization period did not significantly alter the treatments, and the replicates within each treatment were similar. Although the formalin treatment (III-SF) indicates that abiotic processes decreased the fixed amounts of detritus initially added to the containers, this abiotic loss did not affect the experimental design because final detritus quantities were similar to the original fixed levels. In addition, the formalin treatment demonstrates that this abiotic loss of detritus did not change the initial 2:1 fine to medium detritus ratio.

5.5.2 Effect of Substrate Manipulation on Macroinvertebrate Colonization

The design of the substrate experiment allowed the influence of substrate particle size upon macroinvertebrate colonization to be delimited because the detritus source and conditioning in the substrates was carefully standardized, and sedimentation did not change experimental conditions. Despite the wide range of particle size and substrate heterogeneity, interstitial space, surface area and intra-substrate current which the substrate types spanned, only three taxa exhibited significant differences between the treatments. The significant differential colonization of substrates by Thienemannimyia was associated with the slightly lower detritus retention in II-S, but the colonization of the other two taxa did not correspond to any trend of the measured substrate parameters (interstitial space, intra-substrate current, surface area). The lack of correlation between macroinvertebrate distribution and substrate surface area, which was similarly recorded by Rabeni and Minshall (1977), suggests the transformation of macroinvertebrate abundance to density per unit surface area (sensu Reice 1980) is not warranted.

A significant reduction in macroinvertebrate biomass and density resulted when alder detritus was absent (VI-S) from the pebble and cobble substrate, compared to III-S which had identical substrate, but with detritus added. Thus, in the Carnation Creek experiments detritus was a more important microdistribution factor than substrate composition. Although the amount of detritus was relatively constant between treatments I-S to V-S, correlation analyses showed that a few detritivores were influenced by even the small differences in the amounts of fine and medium detritus in these substrates (Table 15).

Clearly, the importance of alder detritus as a microdistribution factor is related to its use by detritivores as a high-quality food resource, since community respiration was largely attributable to microbes associated with the detritus, and biotic processing increased the fine to medium detritus ratio.

Equivocal results were obtained in earlier substrate experiments (Williams and Mundie 1978; Wise and Molles 1979; Khalaf and Tachet 1980; Rabeni and Minshall 1977; Reice 1980) because the influence of detritus and substrate composition could not be separated. These studies found that the highest macroinvertebrate density or biomass occurred in the gravel to pebble substrate size range (10-40 mm), or in slightly larger substrates (16-64 mm; Allen 1975). Indeed, Rabeni and Minshall (1977) hypothesized that high macroinvertebrate abundance in gravel and cobble reflects the greater accumulation of detritus by these substrates, rather than the direct effect of substrate particle size. However, they could not prove this with their experimental design. The Carnation Creek experiment demonstrated that when detritus quality and quantity were standardized, the density and biomass of detritivores was not affected by differences in substrate composition ranging from large gravel to small pebbles.

5.5.3 Effect of Detritus Manipulation on Macroinvertebrate Colonization

Biomasses and densities of 12 of the 20 macroinvertebrate taxa were significantly altered when detritus quality and quantity were manipulated in a substrate of fixed composition. The responses of seven of the remaining eight taxa could not be established because they were rare and had high variances. However, the collector-gatherer, Baetis tricaudatus, appeared unaffected by detritus treatments because in Carnation Creek this mayfly collects periphyton (pers. obs.), which was equally abundant in all five treatments.

Long-term (20-25 weeks) conditioning of mixed douglas-fir (Pseudotsuga menziesii (Mirbel)) and hemlock leaf packs can result in rapid processing by the shredder, Lepidostoma sp (Sedell, Triska, Hall, Lyford and Anderson 1974). However, in Carnation Creek microbial activity (as indicated by community respiration) on hemlock detritus was not significantly different from the activity in the no detritus treatment, even though the hemlock had been conditioned for 5 weeks and then shredded to increase the surface area available for microbial colonization. The low degree of biological processing of this poor-quality food resource was further indicated by the minimal increase in ultra-fine detritus in the hemlock treatment (Figure 15), and the unchanged fine to medium detritus ratio. Chironomidae colonizing the hemlock were either shredder or collector detritivores, but their distribution and abundance was not affected by hemlock detritus since their density and biomass was similar to values recorded for the no detritus treatment. In contrast, Ephemeroptera abundance decreased on hemlock detritus compared to

the no detritus treatment, probably due to toxic leachates similar to those recorded from western red cedar (Peters, Dawson, Hrutfiord and Whitney 1976).

Alder detritus is known to be a high quality food source and is rapidly processed by detritivores (Anderson and Sedell 1979). Even poorly conditioned leaves stimulate detritivore growth (Anderson and Grafius 1975). The significant increase of ultra-fine detritus in both alder treatments, and the increased fine to medium detritus ratio compared to the no detritus treatment, similarly demonstrates the rapid processing of alder detritus in Carnation Creek. Greater microbial activity on the alder substrate, compared to the hemlock and no detritus treatment, also indicates its high food quality. The abundances of 9 of 20 genera were positively affected by alder detritus since they colonized substrates containing low quantities of high-quality alder in higher densities and biomasses than substrates with equivalent amounts of hemlock, or without detritus. When the amount of alder detritus was doubled, mean biomass per individual of Chironomidae was highest, although their densities decreased significantly. In comparison, the densities and biomasses of some taxa decreased to levels below the no detritus treatment in either the high alder treatment (two species of Ephemeroptera), or both the high and low alder treatments (three taxa of Chironomidae). These decreased densities and biomasses in the alder treatments are likely a result of the effects of biotic (e.g. competitive interactions) or abiotic (e.g. low dissolved oxygen in the high alder treatment) environmental factors.

Macroinvertebrate responses to detritus are affected by the size of detritus particles in addition to the quality and quantity of the detritus. When large leaf strips (5 - 10 mm) were added to the substrate (Peckarsky 1980), or when leaf packs of whole leaves were placed on the sediment surface (Reice 1980), only shredder distribution differed with respect to the presence or absence of detritus. Egglishaw (1964) and Rabeni and Minshall (1977) used natural stream detritus of an unknown particle size ratio and suggested densities of some collector and shredder taxa were related to detritus amounts. The Carnation Creek study established that small high quality particles (i.e. 230-850 µm in diameter) are a major determinant of shredder and collector detritivore density and biomass. Thus, macroinvertebrate microdistribution studies which have excluded particles in the 230-850 µm diameter range (e.g. Egglishaw 1964; Rabeni and Minshall 1977; Reice 1980; Peckarsky 1980) certainly underestimate the importance of detritus.

The detritus experiment demonstrates that within identical substrate types both the quality and quantity of detritus can be an important determinant of macroinvertebrate distribution and abundance, and that high-quality alder detritus has a greater effect than poor-quality hemlock. The response by macroinvertebrates to detritus type varied with each taxon considered, and even among members of the collector-gatherer or shredder functional feeding groups. Numerous studies have concluded that

substrate was the major determinant of macroinvertebrate microdistribution without measuring or experimentally controlling detritus (Allen 1975; Minshall and Minshall 1977; Williams and Mundie 1978; Khalaf and Tachet 1980; Williams 1980). Substrate composition may be an important microhabitat determinant for trophic groups such as filter-feeders (Khalaf and Tachet 1980), but detritivore microdistribution appears to depend upon detritus quality and quantity because substrate particle size and detritus accumulation often are not related.

6. EXPERIMENTAL MANIPULATION OF FINE SEDIMENTS

6.1 Introduction

Increases in the proportion of fine sediments in the stream substrate have been shown to have a negative influence on the distribution and abundance of many invertebrates (Chutter 1969; Nuttal and Bielby 1973; Rosenberg and Snow 1975), and high suspended sediment concentrations increase macroinvertebrate drift rates and decrease benthic densities (Rosenberg and Wiens 1978; 1980). In Carnation Creek, the < 9 mm sediments from the eroded streambanks of the reach without a buffer zone have been shown to effect macroinvertebrate communities in at least two ways: during the low discharge period, their deposition and intrusion into the substrate decreased intra-substrate flow and dissolved oxygen; when discharge increased, the downstream movement of the sediments by either suspension or saltation, scoured the substrate (Section 4.4.7).

Scouring of the substrate by saltation is likely a major abiotic perturbation in Carnation Creek because discharge fluctuates rapidly in response to rainfall, with current velocities often being high enough to move sediments by saltation, but not by suspension. However, the effect on the benthos of sediment movement by saltation has never been been investigated. Therefore, over a 24 h period, the response of the benthos to sediment saltation was investigated by experimental manipulation of fine sediments, and the following hypotheses tested:

1) Are the diel drift patterns of macroinvertebrates affected by fine sediment saltation?

2) Does the saltation process itself increase macroinvertebrate drift?

3) Is benthic density or composition affected by fine sediment saltation?

6.2 Methods

The sediment saltation experiment was conducted 1 km upstream of site 1480m in an unlogged stream reach (Figure 1), and was situated in a riffle which was divided into two 3 x 3 m sections; the upper section was designated the control riffle and the lower section the treatment riffle. Before the experiment, three replicate benthic and substrate samples were taken from each of the control and treatment riffles following methods of collection and processing detailed in Section 4.2. Four current velocity measurements were also taken along the midpoint of each riffle at this time using the methods in Section 4.2.

Fine sediments for the experimental additions were collected from streambank gravel bars near the experimental riffles and taken to the laboratory where sediment particles < 0.5 mm and all organic detritus were removed by washing. Only sediment particles between 0.5-2.0 mm were retained for the experiment because these sediments have a relatively short residency time of 1-3 years in Carnation Creek (Scriviner and Brownlee 1980), and are easily transported downstream by saltation.

The experiment was initiated on 15 August 1979 at 1500 h by placing a wooden frame (0.25 m^2) with 20 cm sides onto the substrate of the lower (treatment) riffle so that water flow was momentarily stopped. An ample amount of fine sediment was evenly distributed within the enclosed area to increase the proportion of this particle size in the substrate by 10% (i.e. from 26% to 36%). When the sediments had settled (< 15 s), the frame was gently moved to the adjacent 0.25 m^2 area of riffle, and the process repeated until the entire surface of the treatment riffle had a uniform layer of fine sediments.

Immediately after the introduction of sediments, diurnal macroinvertebrate drift collections from both the control and treatment riffle sections were begun, and the drift nets (15x15 cm; 230 µm mesh) emptied every three hours for a 24 h period. Drift samples were preserved and processed as described in Section 4.2.1. The experiment was terminated 24 h after the sediment additions to the treatment riffle, with three benthic and substrate samples, and four current velocity measurements again being taken in both riffles.

Because the vertical distribution of macroinvertebrates in the upper 6 cm of the substrate may influence their response to sediment saltation, the vertical distribution of the macroinvertebrate taxa of Carnation Creek was determined on 17 September 1980 at site TRC. Site TRC was an unlogged site with similar current velocities, substrate composition and macroinvertebrate community composition to the sediment experiment riffle. Sites 1480m and 630m could not be used because they had been logged. Vertical distribution samples of macroinvertebrates were collected by carefully embedding the cylinder sampler (Section 4.2.1) into the upper 3 cm of substrate, agitating the enclosed substrate (0-3 cm), and emptying the collection net without moving the sampler. With the cylinder sampler still in the same location, the sampler was further embedded and the substrate between 3-6 cm disturbed, and the net emptied. Vertical distribution samples were preserved and processed as outlined in Section 4.2.1.

6.3 Sediment Experiment Results

Current velocities (31-50 cm/s) in the control and treatment riffles were similar before and after the experiment and, in the treatment riffle, rapidly moved the added sediment. Visual observations of the 6 cm water column above the substrate revealed that, during the experiment, sediment particles were not

moved by suspension. Thus, saltation was the only mechanism which removed sediments from the treatment riffle. Within 24 h after the sediment additions, saltation had removed 50% of the added sediments, and reduced the total proportion of fine sediments in the treatment riffle from 36% to 31%.

The major taxa found in the drift, experimental riffle benthos, and control riffle benthos were Chironomidae, Alloperla, B. tricaudatus, Cinygmula, Paraleptophlebia and Zapada, and their combined abundance comprised > 80% of both the total benthos and total drift. All other taxa were rare (< 1%) and were excluded from further analyses.

Significantly higher abundances of all six taxa drifted from the treatment section as compared to the control, with two distinct responses of diurnal drift evident. The first response, shown by B. tricaudatus, Chironomidae, Cinygmula and Zapada, was for drift abundance to significantly increase within three hours (1500-1800 h) after the sediments were introduced to the treatment riffle. For the four taxa which exhibited response I, drift abundance from the treatment riffle remained higher than from the control riffle for 12 to 18 h, at which time much of the fine sediment had been removed from the treatment riffle (Figures 18a and 18b; Figure 19a). In the second response, saltation of fine sediments significantly magnified the diel peaks of Alloperla and Paraleptophlebia (Figure 19b) but the diel pattern was similar to the control.

Before the sediment additions, the upper (control) and lower (treatment) riffle sections had similar benthic macroinvertebrate densities, except for Alloperla which had significantly higher densities in the control riffle (Table 18). However, 24 h after the sediments had been added to the treatment riffle, the densities of Alloperla, B. tricaudatus, Cinygmula and Zapada were significantly lower in the treatment riffle, as compared to the control (upper) riffle, or to the lower (treatment) riffle before sediments (Table 18). Sediment saltation reduced total densities in the treatment riffle by > 50% in 24 h.

The vertical distribution samples indicated that although B. tricaudatus, Chironomidae, Cinygmula and Zapada were collected between 3-6 cm under the surface of the substrate at site TRC, these taxa mainly occupied the upper 0-3 cm of the substrate (Table 19). However, at site TRC, Alloperla and Paraleptophlebia were more evenly distributed throughout the upper 6 cm of the substrate (Table 19).

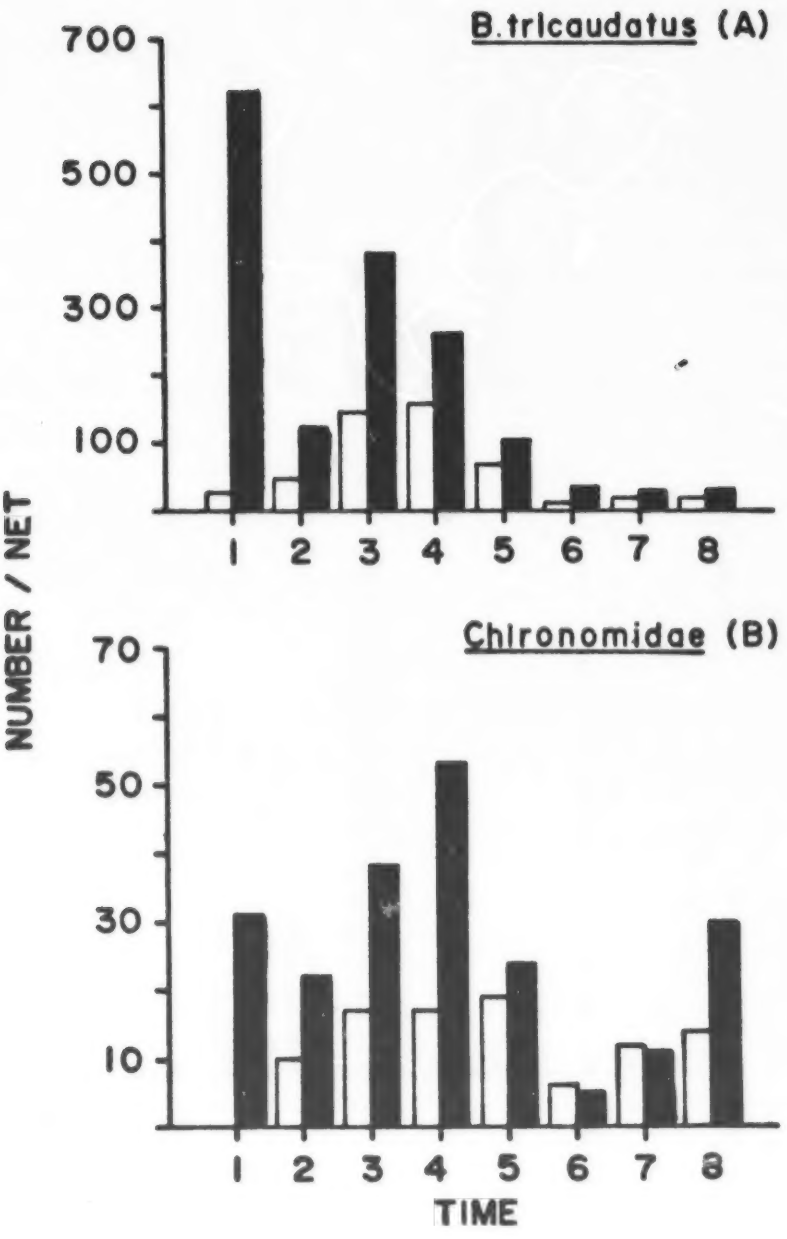

Figure 18. Diurnal pattern (1500-1500 hr) of (A) B. tricaudatus and (B) Chironomidae drifting from the control (white) and sediment treatment (black) riffles during each three hour sampling interval, 15-16 August 1980.

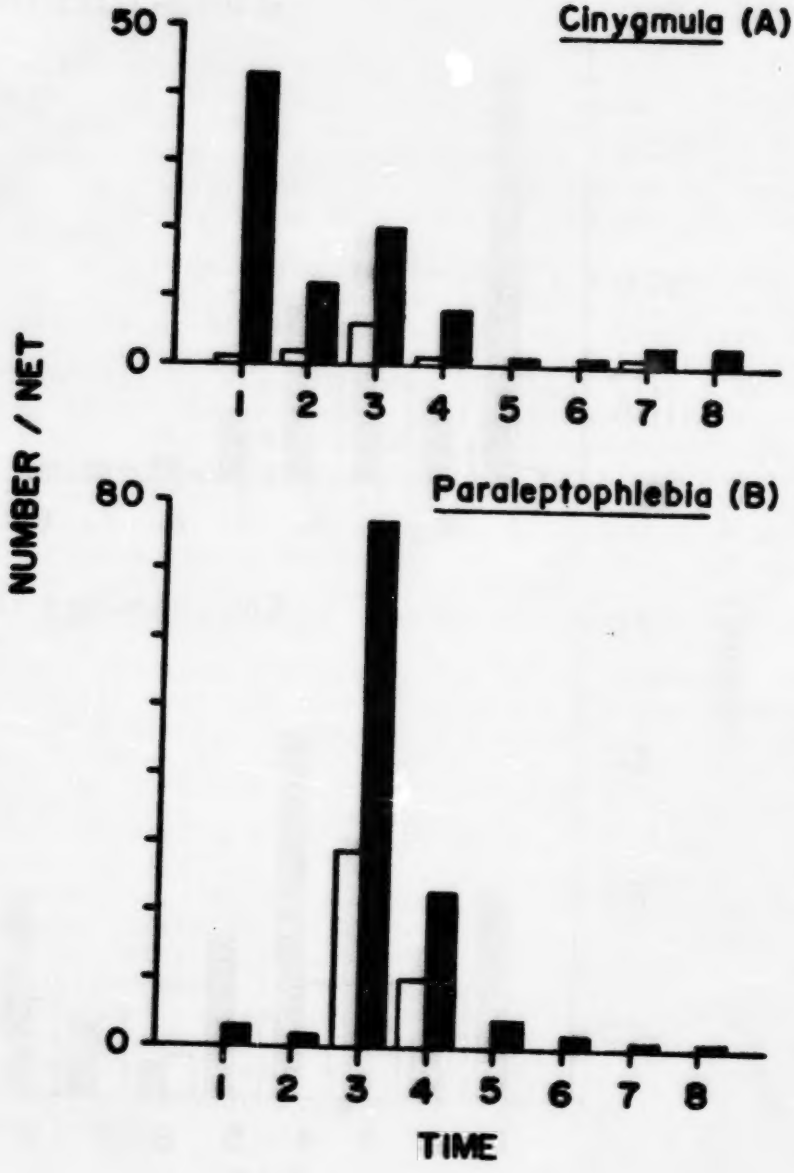

Figure 19. Diurnal pattern (1500-1500 hr) of (A) Cinygmula and (B) Paraleptophlebia drifting from the control (white) and sediment treatment (black) riffles during each three hour sampling interval, 15-16 August 1980.

Table 18. Mean density (no./m^2) of the six most common benthic taxa in the three riffle treatments of the sedimentation experiment. (* indicates a significant difference between the treatments)

Taxa	Riffle Treatment: Upstream Control	Lower Before Sediments	Lower After Sediments
*Alloperla	1367	700	500
*B. tricaudatus	4267	3933	1333
Chironomidae	900	800	533
*Cinygmula	933	900	500
Paraleptophlebia	133	67	33
*Zapada	133	67	33
*Total	7733	6567	2933

Table 19. Densities (no./m^2) of the taxa on the surface (0-3 cm) and deeper (3-6cm) within the substrate which showed drift responses I and II in the sediment experiment. (Samples were taken at site TRC on 80-09-17.)

	Macroinvertebrate Density	
Response I	**0-3 cm**	**3-6 cm**
B. tricaudatus	519	80
Chironomidae	346	133
Cinygmula	819	366
Zapada	87	47
Response II	**0-3 cm**	**3-6 cm**
Alloperla	220	420
Paraleptophlebia	73	67

6.4 Discussion of the Sediment Experiment

The effect of sediment saltation on macroinvertebrates was experimentally determined by adding fine sediments (0.5-2.0 mm) to a riffle substrate in amounts which initially increased the proportional representation of this particle size by 10%. The 10% increase is higher than the observed post-logging increase in sediments < 9 mm at Carnation Creek (Scrivener and Brownlee 1980), but it is clearly within the range of logging-related increases documented by Burns (1972).

Saltation of fine sediments removed 50% of the fine sediments from the treatment riffle within 24 h, and had a detrimental affect on macroinvertebrate densities (Table 18), as the drift rates of the six most abundant taxa increased after sediment addition (Figures 18a and 18b; Figures 19a and 19b). However, the timing and pattern of the increases in drift rates varied, and two basic responses were evident. The first response (I) was for drift from the treatment riffle to increase immediately upon sediment addition, and therefore conceal the natural diurnal pattern which was evident in the drift from the control riffle (Figures 18a and 18b; Figure 19a). In the second response (II), diel periodicity of the drift from the treatment riffle did not change, but the diel peak was significantly increased, as compared to the control riffle values (Figure 19b).

These different drift responses appear to be related to microhabitat differences because, in Carnation Creek, the taxa which show response I are predominantly in the upper 3 cm of the substrate, and those showing response II have equal abundances on the surface (0-3 cm) and deeper (3-6 cm) within the substrate (Table 19). Since the effect of saltation is greatest at the substrate surface and its effects will diminish within the substrate as current velocities decrease, macroinvertebrates in the upper 3 cm exhibiting response I were immediately scoured by saltating sediments. Macroinvertebrates which exhibited drift response II appeared to initially avoid the effects of saltating sediments, perhaps by burrowing deeper into the substrate (below 3 cm). However, the significantly increased diel peak evident in drift response II (Figure 19b) indicates that 6-12 h elapsed before these taxa were affected by the sediment additions. Possible explanations for this time lag effect are that the hyporheic refugium was eventually affected by sediment intrusion, or that these taxa are more active in the 0-3 cm substrate microhabitat during the night.

The Carnation Creek sedimentation experiment demonstrates that the movement of sediments by saltation acts to reduce benthic densities which can potentially change macroinvertebrate composition; suspended sediments can also have this effect on the benthos (Rosenberg and Weins 1978; 1980). Saltation must have a major impact on macroinvertebrate communities in coastal streams because rapid fluctuations in discharge increase the potential for sediment movement. Since clearcutting without buffer strips

increases the rate of streambank erosion and the input of fine sediments (Section 4.4.1), the impact of saltation on the benthos would be greater after logging.

7. SUMMARY

Clearcut logging operations around 1st-3rd order coastal streams can produce significant changes in the abiotic and biotic environmental components of stream ecosystems. Although fish populations of these streams have been studied extensively, little attention has been given to determining the effect post-logging environmental changes have on their benthic macroinvertebrate food source.

Numerous abiotic changes to the stream environment occur as the result of logging operations (in watersheds around coastal streams), but post-logging shifts in stream discharge, bank stability, sedimentation, insolation, water temperature and the terrestrial release of inorganic nutrients are often cited as having the most potential for detrimentally effecting macroinvertebrate communities. The dominant post-logging biotic impact effecting macroinvertebrates is related to shifts in allochthonous and autochthonous energy input, which directly or indirectly act as food resources for the macroinvertebrates.

The Carnation Creek study investigated the effects of two different logging treatments on macroinvertebrate communities. In the site 630m stream reach, logging followed normal west coast logging practices with adherence to the British Columbia Forest Service Watershed Protection Clause (P 1). Clause P 1 states that trees shall not be felled into or yarded through the stream, but allows merchantable timber to be removed from around the stream by using jacks and cables (MacMillan Bloedel Ltd. 1979). Therefore, logging operations at site 630m left a partial leave strip (i.e. buffer zone) of forest that contained only non-merchantable timber.

Clause P 1 was waived along the site 1480m stream reach (MacMillan Bloedel Ltd. 1979), and this resulted in a more severe logging treatment with the forest clearcut to the streambank. Additionally, all the merchantable timber debris in the stream prior to logging was removed during the yarding process (Toews and Moore 1982). Thus, without the P 1 clause in effect, logging activities were not just restricted to clearcutting the streambank, but also included the removal of many of the large, stable debris dams along the site 1480m stream reach.

A major abiotic impact of logging on the Carnation Creek stream ecosystem was the rapid streambank erosion along the stream reach without a buffer zone (site 1480m). This sediment input caused a significant increase in the proportion of < 9 mm sediments in the substrate, and the downstream transport of these < 9 mm sediments, by suspension or saltation, even increased their proportions at site 630m, which had a buffer zone and stable streambanks. Although re-vegetation of the clearcut streambanks is complete after three years, and sediments < 2.38 mm are flushed away within 3 years, logging without a buffer zone channelized this reach, so the post-logging streambed will be scoured more frequently than before. Thus, although streambank destabilization was the major source of increased

post-logging sedimentation in Carnation Creek, apparently it could have been eliminated or prevented by leaving a 10 m wide buffer zone on the streambank with natural debris dams (i.e. logging with P 1 clause restrictions)

Road construction is generally recognized as a major source of logging-related sedimentation (Burns 1972; Gibbons and Salo 1973), but in Carnation Creek this was not observed because roads were placed well away from the stream. Although suspended sediments may have been temporarily increased during rainstorms at the time of road construction, the proportion of fine sediments in the streambed substrate was not affected by these short-term increases of suspended sediments (Toews personal communication). Furthermore, unlike other streams, post-logging mass-wasting (e.g. slumping or landslides in the Carnation Creek watershed has not been near enough to the stream to cause sedimentation to the streambed (Hartman personal communication).

Logging increased the light available for photosynthesis by opening the forest canopy, but as compared to pre-logging estimates, post-logging algal biomass did not significantly increase because phosphorus remained the limiting factor for primary production. Therefore, unlike the coastal streams of California and Oregon, post-logging autochthonous primary production in Carnation Creek did not counterbalance the significant post-logging loss of allochthonous leaf litter input.

Since logging significantly reduced the the input of deciduous and coniferous leaf litter to the stream, even in the reach with a buffer zone, the standing crop of benthic detritus also decreased at both logged sites. However, the post-logging decrease was significantly less in the reach with a buffer zone. If buffer zones are to maintain the normal levels of allochthonous input and benthic detritus standing crop observed for coastal streams, the width of the buffer strip must be wider than the 10 m zone left along Carnation Creek, and selective logging prohibited in this zone.

Clearcutting of the Carnation Creek watershed did not alter the seasonal trends of macroinvertebrate community (species) composition. Throughout the pre- and post-logging period, seasonal changes in benthic composition were strongly affected by the seasonal periods of high, low and transitional discharge. During the high discharge period (November to March), scouring reduced densities of all benthic macroinvertebrate taxa, and changed benthic community composition by reducing the densities of some taxa more than others. Densities of most taxa increased during the low discharge period (April to October), as the macroinvertebrate species in Carnation Creek have adapted their life histories to utilize this annually recurring period of maximum food abundance and substrate habitat stability for the time of maximum growth and reproduction.

Trophic guild composition in Carnation Creek did not follow the predictions of the River Continuum Concept. Shredders were never numerically important in Carnation Creek, because the benthic communities were dominated before and after logging by collectors, collector-scrapers and collector-predators during all

three seasonal periods. As FPOM is the primary food source for macroinvertebrates of these three trophic guilds, and since few shredders were present to comminute CPOM, the formation of FPOM from CPOM in Carnation Creek must largely occur by physical abrasion and/or microbial decomposition.

The winter was an annually recurring period of streambed perturbation and low benthic density, but at site 1480m without a leave strip, winter scouring caused greater decreases in macroinvertebrate density after logging because of the increased input of < 9 mm sediments from the eroded streambanks. The significantly reduced macroinvertebrate densities at site 1480m in the summer and transitional periods, as compared to the pre-logging values, were caused by the intrusion of < 9 mm sediments into the stream substrate which reduced the available habitat for macroinvertebrates. However, the reduced allochthonous energy input at site 1480m lowered the summer and transitional period densities.

Streambank erosion at site 1480m also caused density reductions in the winter at site 630m because of the downstream transport of the < 9 mm sediments. However, the effects of winter scouring were less severe at site 630m because of the buffer zone and the retention of the natural debris dams. The detrimental effects of logging on macroinvertebrates were also reduced at site 630m in the summer and transitional periods. As the major environmental difference between these sites was the higher allochthonous input from the streambank of site 630m, the greater post-logging decrease in total density at site 1480m in the summer and transitional periods appears to be the result of the lower post-logging standing crop of detritus.

Substrate particle sizes ranging from homogeneous gravel to a heterogenous mixture of gravel, pebbles and cobbles did not significantly affect the biomasses or densities of most macroinvertebrate taxa (16 of 19) when detritus quality and quantity in the different substrate mixtures was standardized. In the pebble and cobble substrate without the standardized detritus, macroinvertebrate biomass and density was significantly lower as compared to the identical substrate with detritus added. Thus, the prime importance of detritus as a microdistribution factor was established, and it was concluded that the differential colonization of substrates demonstrated for macroinvertebrate taxa in other substrate experiments was due to differences in organic sedimentation, rather than to differences in substrate particle size composition. Since the substrate particle size range used in the Carnation Creek experiment was similar to the range found in a natural riffles, logging-related changes in substrate composition would not significantly alter macroinvertebrate biomass or density, except when sedimentation reduced the amount of habitat available to macroinvertebrates.

Manipulation of detritus quality and quantity in a substrate of fixed composition further demonstrated that macroinvertebrate microdistribution was significantly affected not only by the quantity of detritus, but also by detritus quality. Generally, alder was a high quality detritus and hemlock was low quality,

but the responses to detritus quality and quantity varied between taxa. The responses were not always predictable, even among members of the same functional feeding groups. However, from this experiment it is clear that significant decreases in benthic detritus quantity which can result from clearcutting the riparian vegetation (particularly deciduous vegetation) will decrease detritivore density and biomass.

Increased input of fine sediments is a major impact of logging. Through experimental sediment addition, it was determined that fine sediment saltation increased macroinvertebrate drift and decreased benthic density. The timing and pattern of the increases in drift varied and were related to the vertical distribution of the taxa within the substrate. Since clearcutting without buffer zones increased streambank erosion and the input of fine sediments, the impact of saltation on the benthos would be greater after clearcut logging, particularly in the winter discharge period.

In conclusion, the Carnation Creek investigation establishes that clearcutting without adherence to the P 1 clause decreases benthic densities primarily because of the increased input of fine sediments from eroded streambanks without buffer zones. Detrimental effects of these fine sediments varied between scouring of the substrate in the winter, and intrusion into the substrate during the summer and transitional periods. Short-term (24 h) sediment additions further indicated that sediment saltation is a significant mechanism by which macroinvertebrates are scoured from the substrate.

Post-logging decreases in macroinvertebrate density were not completely prevented by the presence of a < 10 m wide buffer zone and natural debris dams, but the detrimental effects were less pronounced. In the buffer zone, the effects of winter scouring on macroinvertebrates were reduced, and in the summer and transitional periods, allochthonous litter from the riparian vegetation provided a greater amount of food for macroinvertebrate detritivores, compared to the reach with a clearcut streambank. Manipulative experiments demonstrated that, in Carnation Creek and likely other similar coastal streams, detritus quality and quantity have a greater effect on macroinvertebrate distribution than does substrate particle size.

It is important that buffer zones and natural debris dams be left along coastal streams, and that the buffer zone is wide enough to provide the normal pre-logging levels of allochthonous litter input. However, it is beyond the scope of this study to indicate the optimal buffer strip width for coastal streams, though it is clear that logging with the P 1 clause in effect prevents streambank destabilization by leaving < 10 m buffer zone. Furthermore, the effectiveness of a < 10 m buffer zone in preventing logging-related impacts to the stream would be increased if selective logging of merchantable timber in this zone were prohibited, as logging in the buffer zone greatly reduces leaf litter input to the stream.

Thus, because the streambank of coastal streams provides important energy subsidies to macroinvertebrate communities, and

mediates sediment inputs to the stream, logging of the streambank in coastal streams like Carnation Creek is detrimental to macroinvertebrates. Clearly, as salmonid fry utilize macroinvertebrates as a food resource, management guidelines must protect the streambank interface with the forest if coastal streams are to be maintained as productive salmon fry habitat.

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Appendix I: Mean Monthly Water Temperature (C°) at B and C weirs over the period 1974 to 1981.

		MONTH											
		J	F	M	A	M	J	J	A	S	O	N	D
1974	B	3.2	4.0	3.7	5.5	6.6	9.2	10.2	11.2	10.7	8.5	6.8	5.9
	C	3.0	3.9	3.9	5.9	7.1	9.3	10.5	11.9	12.0	8.7	6.7	6.1
1975	B	3.8	3.4	3.9	4.7	7.1	9.5	11.4	10.8	10.1	9.0	6.7	6.6
	C	3.6	2.8	3.4	4.5	7.4	9.5	11.4	11.2	10.9	8.8	6.0	4.2
1976	B	4.5	3.8	3.6	4.7	6.9	8.4	10.1	10.8	10.5	8.7	7.8	6.6
	C	4.1	3.6	3.7	5.1	7.4	8.5	10.6	11.4	11.0	9.2	7.6	6.1
1977	B	4.6	6.1	5.2	6.6	8.4	10.9	12.1	12.6	11.3	9.2	6.4	5.0
	C	3.5	5.9	4.7	6.1	7.6	9.8	10.8	12.7	10.7	8.7	5.5	4.2
1978	B	5.0	5.6	6.3	7.3	9.1	12.0	13.3	12.8	11.2	10.2	6.4	4.5
	C	4.6	5.2	8.4	9.2	7.7	11.1	12.3	12.0	10.8	9.6	5.1	3.9
1979	B	3.0	3.7	5.9	7.5	10.6	12.7	13.9	15.2	12.6	10.5	7.6	6.7
	C	1.7	3.4	5.3	6.1	8.7	10.0	11.9	13.2	12.0	10.1	6.6	6.4
1980	B	3.7	4.6	5.6	6.6	10.9	11.9	13.3	14.1	12.5	10.7	8.2	6.5
	C	3.0	4.2	4.8	6.5	8.8	9.8	11.4	12.0	11.1	9.6	7.7	5.9
1981	B	7.2	6.5	8.0	7.6	10.9	11.5	14.1	15.0	13.3	-	-	-
	C	7.3	5.4	6.3	6.3	8.5	9.6	12.0	13.4	11.7	8.6	-	-

Appendix II Mean current velocity (cm/s) 2.5 cm above the substrate at 630m, 1480m and TRC on the 1980 sampling dates.

Sampling Date	950 m	1720 m	C2
January 23	33	29	33
March 30	35	25	31
May 13	26	20	18
June 17	23	21	35
July 17	39	40	26
August 17	23	16	23
September 17	30	20	21
November 11	36	32	33

Appendix III. Mean density (no./0.1m^2) and standard error of the diagnostic taxa at site 630m during the summer.

	Pre-Logging			Post-Logging			
Taxa	1974	1975	1976	1977	1978	1979	1980
Alloperla	271 ± 56	152 ± 40	173 ± 46	182 ± 12	130 ± 20	115 ± 34	80 ± 9
B. tricaudatus	130 ± 51	240 ± 95	94 ± 31	76 ± 38	83 ± 33	41 ± 10	110 ± 25
Capnia	21 ± 12	8 ± 2	3 ± 2	0 ± 0	4 ± 2	4 ± 1	9 ± 3
Chironomidae	267 ± 61	218 ± 50	273 ± 126	61 ± 3	165 ± 29	237 ± 21	177 ± 48
Cinygmula	107 ± 14	183 ± 37	134 ± 54	150 ± 5	101 ± 10	178 ± 21	336 ± 34
Epeorus	61 ± 17	46 ± 15	98 ± 44	95 ± 50	11 ± 5	8 ± 6	13 ± 4
K. perdita	4 ± 2	2 ± 1	12 ± 5	6 ± 1	2 ± 1	5 ± 1	0 ± 0
Leuctra	13 ± 5	10 ± 4	11 ± 3	2 ± 1	6 ± 3	12 ± 4	18 ± 6
Nemoura	10 ± 4	12 ± 3	21 ± 5	2 ± 1	9 ± 5	3 ± 1	15 ± 3
Paraleptophlebia	16 ± 7	19 ± 9	92 ± 26	5 ± 3	38 ± 11	88 ± 22	46 ± 12

Appendix IV. Mean density (no./0.1m^2) and standard error of the diagnostic taxa at site 1480m during the summer.

Taxa	Pre-Logging			Post-Logging			
	1974	1975	1976	1977	1978	1979	1980
Alloperla	213 ± 21	199 ± 29	221 ± 70	68 ± 5	38 ± 8	42 ± 23	18 ± 5
B. tricaudatus	217 ± 95	245 ± 62	118 ± 46	87 ± 23	142 ± 40	32 ± 14	146 ± 58
Capnia	14 ± 7	14 ± 9	5 ± 3	4 ± 2	0 ± 0	0 ± 0	8 ± 3
Chironomidae	334 ± 147	492 ± 118	125 ± 29	151 ± 51	114 ± 39	182 ± 26	151 ± 22
Cinygmula	148 ± 26	194 ± 25	132 ± 55	100 ± 8	109 ± 13	80 ± 20	222 ± 23
Epeorus	103 ± 40	75 ± 20	63 ± 23	21 ± 7	12 ± 3	21 ± 13	14 ± 5
K. perdita	6 ± 3	3 ± 1	10 ± 5	2 ± 1	0 ± 0	0 ± 0	0 ± 0
Leuctra	14 ± 5	6 ± 2	4 ± 2	3 ± 2	0 ± 0	1 ± 1	1 ± 1
Nemoura	17 ± 7	52 ± 23	34 ± 12	3 ± 1	26 ± 9	14 ± 5	27 ± 6
Paraleptophlebia	23 ± 10	57 ± 17	50 ± 14	18 ± 8	40 ± 20	23 ± 9	45 ± 15

Appendix V. Mean density (no./0.1m^2) and standard error of the diagnostic taxa at site TRC during the summer.

	Pre-Logging			Post-Logging			
Taxa	1974	1975	1976	1977	1978	1979	1980
Alloperla	132 ± 29	85 ± 20	127 ± 32	72 ± 8	63 ± 14	68 ± 23	93 ± 9
B. tricaudatus	16 ± 5	33 ± 10	44 ± 11	18 ± 3	65 ± 19	109 ± 32	111 ± 20
Capnia	1 ± 1	1 ± 1	0 ± 0	5 ± 3	1 ± 1	2 ± 1	2 ± 1
Chironomidae	147 ± 18	217 ± 38	186 ± 88	97 ± 60	89 ± 14	628 ± 161	85 ± 11
Cinygmula	85 ± 22	115 ± 23	75 ± 25	39 ± 10	47 ± 3	45 ± 12	110 ± 14
Epeorus	14 ± 8	16 ± 5	45 ± 27	31 ± 19	10 ± 3	23 ± 13	45 ± 12
K. perdita	3 ± 1	3 ± 1	12 ± 3	10 ± 2	3 ± 2	2 ± 1	16 ± 4
Leuctra	15 ± 2	3 ± 1	30 ± 11	9 ± 2	6 ± 1	6 ± 3	16 ± 5
Nemoura	2 ± 1	5 ± 1	27 ± 8	7 ± 5	23 ± 7	16 ± 10	14 ± 3
Paraleptophlebia	11 ± 5	11 ± 3	30 ± 8	14 ± 2	16 ± 4	13 ± 6	27 ± 4

Appendix VI. Mean density (no./0.1m^2) and standard error of the diagnostic taxa at site 630m during the transitional period.

Taxa	Pre-Logging			Post-Logging		
	1974	1975	1976	1977	1978	1979
Alloperla	223 ± 28	162 ± 44	348 ± 103	186 ± 37	188 ± 31	82 ± 7
B. tricaudatus	44 ± 7	123 ± 51	74 ± 36	140 ± 46	91 ± 15	155 ± 22
Capnia	40 ± 23	17 ± 10	5 ± 2	16 ± 2	22 ± 18	21 ± 10
Chironomidae	224 ± 33	345 ± 147	410 ± 250	290 ± 111	150 ± 60	168 ± 43
Cinygmula	169 ± 24	160 ± 11	630 ± 163	171 ± 53	222 ± 43	413 ± 91
Epeorus	60 ± 36	11 ± 6	163 ± 9	50 ± 29	10 ± 6	74 ± 27
K. perdita	2 ± 1	7 ± 2	20 ± 15	5 ± 2	6 ± 2	0 ± 0
Leuctra	22 ± 12	15 ± 7	9 ± 6	8 ± 5	7 ± 5	21 ± 9
Nemoura	4 ± 2	8 ± 2	3 ± 2	11 ± 4	5 ± 2	6 ± 4
Paraleptophlebia	24 ± 7	17 ± 9	37 ± 7	39 ± 8	40 ± 13	115 ± 30

Appendix VII. Mean density (no./0.1m^2) and standard error of the diagnostic taxa at site 1480m during the transitional period.

	Pre-Logging			Post-Logging		
Taxa	1974	1975	1976	1977	1978	1980
Alloperla	206 ± 13	188 ± 43	347 ± 45	69 ± 5	44 ± 17	39 ± 6
B. tricaudatus	74 ± 18	157 ± 57	63 ± 7	76 ± 20	28 ± 18	302 ± 96
Capnia	27 ± 13	64 ± 47	2 ± 1	15 ± 9	1 ± 1	12 ± 5
Chironomidae	486 ± 149	827 ± 519	90 ± 1	239 ± 134	57 ± 9	112 ± 21
Cinygmula	142 ± 37	326 ± 172	292 ± 47	218 ± 59	47 ± 8	124 ± 24
Epeorus	67 ± 48	36 ± 21	182 ± 21	14 ± 11	17 ± 8	55 ± 17
K. perdita	3 ± 1	5 ± 2	21 ± 1	3 ± 1	0 ± 0	0 ± 0
Leuctra	27 ± 20	23 ± 9	4 ± 1	5 ± 3	0 ± 0	1 ± 1
Nemoura	16 ± 6	3 ± 1	1 ± 1	3 ± 2	0 ± 0	3 ± 2
Paraleptophlebia	54 ± 26	109 ± 72	49 ± 29	54 ± 30	3 ± 1	71 ± 24

Appendix VIII. Mean density (no./0.1m^2) and standard error of the diagnostic taxa at site TRC during the transitional period.

Taxa	Pre-Logging			Post-Logging		
	1974	1975	1976	1977	1978	1980
Alloperla	77 ± 14	192 ± 25	216 ± 5	113 ± 30	71 ± 7	71 ± 9
B. tricaudatus	9 ± 7	34 ± 10	109 ± 23	32 ± 7	18 ± 7	41 ± 8
Capnia	1 ± 1	4 ± 2	3 ± 1	10 ± 5	4 ± 2	3 ± 1
Chironomidae	140 ± 36	412 ± 134	508 ± 179	123 ± 56	52 ± 16	60 ± 9
Cinygmula	47 ± 32	187 ± 52	82 ± 1	145 ± 84	54 ± 14	79 ± 15
Epeorus	34 ± 20	91 ± 50	298 ± 45	28 ± 27	36 ± 18	65 ± 12
K. perdita	2 ± 1	10 ± 3	25 ± 1	14 ± 5	6 ± 1	10 ± 3
Leuctra	12 ± 7	31 ± 4	56 ± 31	36 ± 8	5 ± 2	26 ± 6
Nemoura	3 ± 2	8 ± 4	24 ± 3	13 ± 12	6 ± 3	5 ± 2
Paraleptophlebia	25 ± 2	22 ± 11	33 ± 25	22 ± 9	8 ± 2	13 ± 3

Appendix IX. Mean density (no./0.1m^2) and standard error of the diagnostic taxa at site 630m during the winter.

Taxa	Pre-Logging 1974	Pre-Logging 1975	Pre-Logging 1976	Post-Logging 1977	Post-Logging 1978	Post-Logging 1980
Alloperla	151 ± 46	143 ± 29	71 ± 3	98 ± 20	145 ± 16	71 ± 6
B. tricaudatus	12 ± 4	36 ± 12	52 ± 7	88 ± 29	101 ± 30	96 ± 10
Capnia	5 ± 4	4 ± 2	14 ± 8	11 ± 4	19 ± 8	3 ± 1
Chironomidae	132 ± 59	257 ± 92	65 ± 17	104 ± 41	178 ± 64	48 ± 8
Cinygmula	63 ± 21	166 ± 35	218 ± 37	184 ± 48	76 ± 11	52 ± 6
Epeorus	5 ± 2	4 ± 1	8 ± 4	17 ± 10	4 ± 1	11 ± 3
K. perdita	3 ± 1	5 ± 1	3 ± 1	3 ± 1	3 ± 2	0 ± 0
Leuctra	19 ± 9	17 ± 3	13 ± 8	6 ± 3	4 ± 3	2 ± 1
Nemoura	2 ± 1	4 ± 1	2 ± 1	2 ± 1	2 ± 1	2 ± 1
Paraleptophlebia	7 ± 3	12 ± 6	8 ± 5	21 ± 7	22 ± 6	2 ± 1

Appendix X. Mean density (no./0.1m^2) and standard error of the diagnostic taxa at site 1480m during the winter.

	Pre-Logging			Post-Logging		
Taxa	1974	1975	1976	1977	1978	1980
Alloperla	151 ± 20	148 ± 25	130 ± 22	101 ± 20	31 ± 9	16 ± 3
B. tricaudatus	24 ± 4	42 ± 11	101 ± 28	232 ± 101	113 ± 32	57 ± 12
Capnia	1 ± 1	1 ± 1	19 ± 12	8 ± 3	4 ± 2	5 ± 2
Chironomidae	166 ± 38	334 ± 87	81 ± 41	345 ± 172	37 ± 11	7 ± 2
Cinygmula	161 ± 50	85 ± 26	162 ± 30	180 ± 62	48 ± 11	25 ± 4
Epeorus	39 ± 20	13 ± 5	13 ± 7	56 ± 29	8 ± 4	4 ± 2
K. perdita	4 ± 1	9 ± 2	7 ± 2	4 ± 1	3 ± 1	0 ± 0
Leuctra	11 ± 4	12 ± 2	19 ± 10	8 ± 3	0 ± 0	0 ± 0
Nemoura	3 ± 1	1 ± 1	1 ± 1	1 ± 1	1 ± 1	0 ± 0
Paraleptophlebia	18 ± 7	25 ± 8	26 ± 13	43 ± 21	4 ± 2	2 ± 1

Appendix XI. Mean density (no./0.1m^2) and standard error of the diagnostic taxa at site TRC during the winter.

	Pre-Logging			Post-Logging		
Taxa	1974	1975	1976	1977	1978	1980
Alloperla	133 ± 21	158 ± 59	100 ± 12	87 ± 14	86 ± 20	59 ± 8
B. tricaudatus	9 ± 3	12 ± 5	26 ± 10	32 ± 13	35 ± 11	24 ± 5
Capnia	0 ± 0	0 ± 0	7 ± 4	7 ± 3	3 ± 2	5 ± 2
Chironomidae	156 ± 32	202 ± 70	120 ± 27	49 ± 8	88 ± 36	38 ± 7
Cinygmula	67 ± 16	48 ± 12	103 ± 31	75 ± 13	61 ± 23	64 ± 13
Epeorus	57 ± 32	29 ± 14	43 ± 23	38 ± 16	22 ± 5	17 ± 5
K. perdita	9 ± 2	4 ± 1	4 ± 2	7 ± 2	8 ± 3	17 ± 3
Leuctra	24 ± 4	16 ± 5	24 ± 9	12 ± 3	16 ± 7	9 ± 2
Nemoura	5 ± 1	3 ± 1	5 ± 2	3 ± 1	5 ± 2	7 ± 3
Paraleptophlebia	9 ± 2	10 ± 3	10 ± 2	9 ± 3	14 ± 8	9 ± 4

Appendix XII. Mean density (no./0.1m^2) and standard error of the trophic guilds at site 630m during the summer.

	Pre-Logging			Post-Logging			
Trophic Guild	1974	1975	1976	1977	1978	1979	1980
Collector	491 ± 192	516 ± 141	563 ± 173	287 ± 83	347 ± 61	444 ± 57	384 ± 79
Collector-Scraper	207 ± 44	233 ± 48	234 ± 98	244 ± 55	114 ± 14	186 ± 22	350 ± 31
Collector-Predator	271 ± 56	152 ± 40	173 ± 46	182 ± 12	130 ± 20	115 ± 34	80 ± 9
Scraper	1 ± 1	61 ± 44	2 ± 1	0 ± 0	63 ± 49	9 ± 4	22 ± 15
Shredder	52 ± 23	41 ± 6	48 ± 9	5 ± 1	27 ± 11	43 ± 9	56 ± 13

Appendix XIII. Mean density (no./0.1m^2) and standard error of the trophic guilds at site 1480m during the summer.

Trophic Guild	Pre-Logging			Post-Logging			
	1974	1975	1976	1977	1978	1979	1980
Collector	670 ± 196	876 ± 186	397 ± 74	405 ± 118	360 ± 96	270 ± 45	391 ± 78
Collector-Scraper	268 ± 39	326 ± 47	196 ± 78	136 ± 8	121 ± 13	101 ± 30	240 ± 25
Collector-Predator	213 ± 21	199 ± 29	221 ± 70	68 ± 5	38 ± 8	41 ± 23	18 ± 5
Scraper	1 ± 1	11 ± 6	8 ± 4	1 ± 1	1 ± 1	0 ± 0	1 ± 1
Shredder	59 ± 17	92 ± 27	59 ± 10	11 ± 5	27 ± 9	18 ± 6	41 ± 9

Appendix XIV. Mean density (no./0.1m^2) and standard error of the trophic guilds at site TRC during the summer.

	Pre-Logging			Post-Logging			
Trophic Guild	1974	1975	1976	1977	1978	1979	1980
Collector	306 ± 38	321 ± 46	357 ± 135	182 ± 61	208 ± 28	882 ± 227	286 ± 26
Collector-Scraper	127 ± 18	144 ± 25	131 ± 58	70 ± 15	59 ± 6	68 ± 12	156 ± 14
Collector-Predator	132 ± 29	85 ± 21	127 ± 32	72 ± 8	63 ± 14	68 ± 23	93 ± 9
Scraper	0 ± 0	12 ± 9	11 ± 6	22 ± 15	5 ± 2	1 ± 1	149 ± 47
Shredder	33 ± 6	24 ± 4	71 ± 18	52 ± 26	40 ± 14	64 ± 29	56 ± 12

Appendix XV. Mean density (no./0.1m^2) and standard error of the trophic guilds at site 630m during the transitional period.

	Pre-Logging			Post-Logging		
Trophic Guild	1974	1975	1976	1977	1978	1980
Collector	404 ± 68	585 ± 122	709 ± 284	614 ± 91	425 ± 88	504 ± 76
Collector-Scraper	240 ± 55	268 ± 101	793 ± 171	223 ± 82	235 ± 40	490 ± 72
Collector-Predator	223 ± 28	161 ± 44	348 ± 103	186 ± 37	188 ± 31	82 ± 8
Scraper	5 ± 4	5 ± 5	2 ± 1	2 ± 1	1 ± 1	9 ± 4
Shredder	79 ± 37	49 ± 14	24 ± 1	36 ± 12	41 ± 31	61 ± 18

Appendix XVI. Mean density (no./0.1m^2) and standard error of the trophic guilds at site 1480m during the transitional period.

	Pre-Logging			Post-Logging		
Trophic Guild	1974	1975	1976	1977	1978	1980
Collector	718 ± 197	1234 ± 664	327 ± 50	517 ± 232	136 ± 24	522 ± 129
Collector-Scraper	282 ± 85	527 ± 291	482 ± 64	265 ± 51	65 ± 18	184 ± 23
Collector-Predator	207 ± 13	189 ± 43	347 ± 44	69 ± 5	43 ± 17	39 ± 6
Scraper	5 ± 3	11 ± 9	1 ± 1	2 ± 2	0 ± 0	1 ± 1
Shredder	86 ± 38	95 ± 57	11 ± 5	24 ± 12	1 ± 1	18 ± 5

Appendix XVII. Mean density (no./0.1m^2) and standard error of the trophic guilds at site TRC during the transitional period.

	Pre-Logging			Post-Logging		
Trophic Guild	1974	1975	1976	1977	1978	1980
Collector	295 ± 50	745 ± 178	831 ± 162	274 ± 86	138 ± 24	219 ± 23
Collector-Scraper	147 ± 44	432 ± 60	430 ± 36	184 ± 76	97 ± 10	148 ± 13
Collector-Predator	77 ± 14	191 ± 25	216 ± 5	113 ± 30	81 ± 9	71 ± 9
Scraper	5 ± 4	53 ± 31	16 ± 7	26 ± 15	2 ± 1	38 ± 11
Shredder	26 ± 17	59 ± 11	91 ± 39	66 ± 21	12 ± 1	64 ± 17

Appendix XVIII. Mean density (no./0.1m^2) and standard error of the trophic guilds at site 630m during the winter.

	Pre-Logging			Post-Logging		
Trophic Guild	1974	1975	1976	1977	1978	1980
Collector	220 ± 75	409 ± 113	160 ± 15	314 ± 61	443 ± 106	171 ± 14
Collector-Scraper	72 ± 20	190 ± 29	237 ± 36	215 ± 57	90 ± 11	67 ± 9
Collector-Predator	151 ± 46	143 ± 29	71 ± 4	98 ± 21	145 ± 16	71 ± 6
Scraper	0 ± 0	2 ± 1	3 ± 2	2 ± 1	1 ± 1	1 ± 1
Shredder	29 ± 11	26 ± 3	33 ± 18	20 ± 4	28 ± 10	5 ± 1

Appendix XIX. Mean density (no./0.1m^2) and standard error of the trophic guilds at site 1480m during the winter.

	Pre-Logging			Post-Logging		
Trophic Guild	1974	1975	1976	1977	1978	1980
Collector	314 ± 81	538 ± 104	260 ± 82	703 ± 304	233 ± 70	64 ± 14
Collector-Scraper	227 ± 62	124 ± 35	184 ± 30	239 ± 87	67 ± 14	27 ± 4
Collector-Predator	150 ± 20	148 ± 25	130 ± 22	101 ± 20	31 ± 9	15 ± 3
Scraper	1 ± 1	3 ± 1	26 ± 15	1 ± 1	1 ± 1	0 ± 0
Shredder	17 ± 5	21 ± 4	41 ± 22	18 ± 5	7 ± 4	6 ± 2

Appendix XX. Mean density (no./0.1m^2) and standard error of the trophic guilds at site TRC during the winter.

	Pre-Logging			Post-Logging		
Trophic Guild	1974	1975	1976	1977	1978	1980
Collector	311 ± 33	560 ± 222	206 ± 32	158 ± 19	240 ± 88	136 ± 15
Collector-Scraper	174 ± 23	288 ± 131	153 ± 25	127 ± 14	88 ± 23	92 ± 13
Collector-Predator	133 ± 21	158 ± 59	100 ± 12	87 ± 14	86 ± 20	59 ± 8
Scraper	5 ± 3	7 ± 3	13 ± 4	23 ± 9	11 ± 3	34 ± 14
Shredder	32 ± 5	23 ± 6	45 ± 18	27 ± 5	32 ± 12	33 ± 7

POOR

QUALITY

ORIGINAL